University of Alberta

Saproxylic beetle assemblages in the boreal mixedwood of Alberta: succession, wildfire and variable retention forestry

by

Joshua Michael Jacobs ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Science

Edmonton, Alberta

Fall 2004

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-95777-2
Our file Notre référence
ISBN: 0-612-95777-2

The author has granted a non-exclusive license allowing the Library and Archives Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Acknowledgments

This project was funded by Canadian Forest Products (CANFOR) and Daishowa-Marubeni International Ltd. (DMI) through the Sustainable Forest Management Network (SFMN). Furthermore, this project would have not been possible without John Spence (U of A) and Jan Volney (CFS), Steve Luchkow, (DMI) and Tim Vinge (Canfor), who designed and implemented the EMEND study site.

The knowledge of John Spence and Dave Langor (supervisors) was instrumental in the design of my project and editing of this thesis. I would also like to thank my committee, Ellen MacDonald, Felix Sperling and Bruce Heming, for guidance and comments on the final thesis. The entire Spence lab always provided support, ears to bounce ideas off of and good times when the times weren't always so good. Many people offered their assistance in the identification of the beetles including Karen Cryer, Tim Work, Tyler Cobb, James Hammond, Gerry Hilchie, Ed Fuller, George Ball, and Danny Shpeley. Tim Work and Tyler Cobb contributed to the statistical analysis of this thesis. I would also like to thank Tyler Cobb and Katarzyna Dyszy who provided constructive comments during the writing of the thesis.

I would especially like to acknowledge my parents and family, whose continued support was vital to every aspect of this thesis.

Table of Contents

Chapter 1 Introduction 1
  1.1 The Boreal Mixedwood Forest 1
  1.2 Ecological role of natural disturbances 1
  1.3 Saproxylic insect assemblages 3
  1.4 Adaptive Forest Management 4
  1.5 Objectives of this Thesis 7
  Literature Cited 9

Chapter 2 Stand structure and composition, dead wood quality and saproxylic beetles . 14
  Introduction 14
  Materials and Methods 15
  Results 20
  Discussion 40
  Literature Cited 45
  Appendix 2-A 48

Chapter 3 Attraction of epigaeic and saproxylic beetles to a burned stand 57
  Introduction 57
  Materials and Methods 58
  Results 62
  Discussion 72
  Literature Cited 75
  Appendix 3-A 78
  Appendix 3-B 81

Chapter 4 Effects of Variable Retention Harvesting on Saproxylic Beetle Assemblages 86
  Introduction 86
  Materials and Methods 87
  Results 92
  Discussion 105
  Literature Cited 108
  Appendix 4-A 111

Chapter 5 General Discussion 118
  5.1 Main Findings of the Thesis 118
  5.2 Importance of Coarse Woody Debris (CWD) 120
  5.3 Saproxylic beetle definition and sampling methods. 120
  5.4 Management recommendations and future research 121
  Literature Cited 123

List of Tables

Table 1-1 Experimental design of the EMEND project indicating the number of replicates of each cover type treatment combination. 7

Table 2-1 P values of the Tukey's post hoc test on the different types of CWD across all cover types. * indicates significant differences. 23

Table 2-2 Species richness, chao2 estimate of species richness and species catch for each cover type and tree species 24

Table 2-3 Significant indicators species of girdled or dead aspen or spruce trees in mixedwood stands. 27

Table 2-4 Significant indicators species of different girdled or dead aspen trees in deciduous dominated or co-dominated cover types. 29

Table 2-5 Significant indicator species indicators of spruce trees in coniferous dominated or co-dominated stands. 33

Table 2-6 Significant indicators species of different years in CDOM and MX-Conifer stands trapped on girdled and naturally dead spruce trees 35

Table 2-7 Significant indicators species of terminal nodes on multivariate regression tree. 38

Table 3-1 Species of epigaeic beetles of significant indicator value for each treatment in a prescribed burn. 65

Table 3-2 Species of saproxylic beetles of significant indicator value for each burn severity treatment and for cause of tree mortality (girdled or naturally dead before burning) in a prescribed burn. 71

Table 4-1 Criteria used for classifying CWD at the local level around each trap. 90

Table 4-2 Mean number of pieces of CWD in a 5m radius around each trap. Letters denote significant differences of CWD within each CWD category. 94

Table 4-3 Significant indicator species of harvesting and trap treatments. 103

List of Figures

Figure 1-1 The relative abundance of canopy trees in each of the cover types: DDOM, deciduous dominated; DDOMU, deciduous dominated with a developing coniferous understory; MX, mixedwood; and CDOM; coniferous dominated. 6

Figure 2-1 The relative abundance of canopy trees in each of the cover types: DDOM, deciduous dominated; DDOMU, deciduous dominated with a developing coniferous understory; MX, mixedwood; and CDOM; coniferous dominated. 16

Figure 2-2 Mean volume of downed woody debris (DWD) in each cover type. Error bars represent one standard error above the mean........ 21

Figure 2-3 Density of snags in each cover type. Error bars represent one standard error above the mean. Letters denote differences in overall snag density among cover types. 21

Figure 2-4 Diameter at breast height (DBH) (cm) (+ standard error) of trap trees in each cover type. 22

Figure 2-5 Number and type of pieces of CWD in each of the five cover types. Boxes represent mean number of pieces in 5m radius plot centered on traps, error bars represents 2 standard errors above and below the mean. 23

Figure 2-6 Rarefaction estimates of species in each cover type and trap tree species. 24

Figure 2-7 NMS ordination of 114 species and 12 sample units of aspen and spruce trees in mixedwood stands: A) samples in species space, and B) overlay of species on the initial ordination. Numbers correspond to Table 2-3, species with a significant indicator value to stand and mortality type. 26

Figure 2-8 NMS ordination of 131 species and 18 samples collected in deciduous dominated or co-dominated stands; A) abundance data, and B) presence / absence data. 30

Figure 2-9 NMS ordination of 117 species and 12 samples of spruce trees in coniferous dominated or co-dominated cover types: A) samples in species space, and B) overlay of species on the initial ordination. Numbers correspond to Table 2-5, species with a significant indicator value to stand and mortality type. 32

Figure 2-10 NMS ordination of 114 species and 36 samples in CDOM and MX-Spruce stands: A) samples coded by cover type; B) samples coded by tree mortality; C) samples coded by year, and D) species overlay. 34

Figure 2-11 Catch of saproxylic beetles on girdled and naturally dead trees in conifer dominated and mixedwood cover types........ 36

Figure 2-12 Multivariate regression tree of all sites. Graphs are abundance plots of all 189 saproxylic beetle species. Error 0.57, CV error 0.838, SE 0.0767. 37

Figure 3-1 Rarefaction estimates of species richness of epigaeic beetles in sub-samples of increasing size in skips, light burns and severe burns........ 62

Figure 3-2 Venn diagram showing number of unique and shared species of epigaeic beetles among skips, light burns, and severe burns. Numbers in parentheses indicate total species richness for each treatment. 63

Figure 3-3 Catch of epigaeic beetles standardized to beetles per trap day in skips, light burns and severe burns. Catch for each treatment is divided into Trap A and Trap B. In light burns, Trap A was placed on scorched ground and Trap B was placed in the litter. Error bars represent one standard error above the mean. Total catch (both traps combined) was compared among burn intensities using Tukey's *post hoc* tests, and pairs of bars with the same letter written above indicate no significance at alpha = 0.05. 63

Figure 3-4 NMS ordination of epigaeic beetles in skips, light burns and severe burns. Scores are pooled samples from each treatment and replicate. 64

Figure 3-5 Mean standardized catch of *Sericoda quadripunctata* and *Sericoda bembidioides* one and two years following fire in skips, light burns, and severe burns. Error bars represent one standard deviation above the mean. 66

Figure 3-6 NMS ordination of epigaeic beetles in individual traps (2000 & 2001 data combined) in skips, light burns and severe burns. In light burns, Trap A (dotted polygon) was placed in duff and Trap B (solid polygon) was placed in scorched ground. 67

Figure 3-7 Rarefaction estimate of species richness of saproxylic beetles in sub-samples of increasing size in skips, light burns and severe burns. 68

Figure 3-8 Venn diagram showing unique and shared species of saproxylic beetles in skips, light burns and severe burns. Numbers in parentheses indicate total species richness for each treatment. 68

Figure 3-9 NMS ordination of saproxylic beetles in a burned coniferous stand. Points represent traps on individual trees separated by year of catch. 69

Figure 3-10 NMS ordination of saproxylic beetles in skips, light burns and severe burns: A) first year following fire (2000), and B) second year following fire (2001). Each point represents a single window trap on either a tree killed by girdling or killed naturally before the stand was burned. 70

Figure 4-1 Mean ± 1 SE volume of downed woody debris (DWD) in each treatment. 93

Figure 4-2 Mean ± 1 SE density of snags in each treatment. Capital letters denote overall treatment effects and lowercase letters denote results of Tukey's *post hoc* tests of differences within each treatment. 93

Figure 4-3 Rarefaction curves for: A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores; and D) predators for all harvesting treatments. 96

Figure 4-4 Mean catch rate of: A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores, and D) predators for all harvesting treatments grouped by year. Error bars represent 1 SE above the mean. 96

Figure 4-5 Rarefaction curves for: A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores; and D) predators collected from trees killed by girdling and naturally dead trees. 97

Figure 4-6 Mean catch rate of A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores, and D) predators, collected from trees killed by girdling and naturally dead trees. Error bars represent 1 SE above the mean. 97

Figure 4-7 NMS ordination of wood- and bark- boring beetles: A) year 2000 grouped by harvesting treatment; B) year 2000 grouped by trap treatment; C) year 2001 grouped by harvesting treatment, and D) year 2001 grouped by trap treatment. 99

Figure 4-8 NMS ordination of fungivores: A) year 2000 grouped by harvesting treatment; B) 2000 grouped by trap treatment; C) year 2001 grouped by harvesting treatment, and D) year 2001 grouped by trap treatment. 100

Figure 4-9 NMS ordination of predators: A) year 2000 grouped by harvesting treatment; B) year 2000 grouped by trap treatment; C) year 2001 grouped by harvesting treatment, and D) year 2001 grouped by trap treatment. 102

Chapter 1 Introduction

1.1 The Boreal Mixedwood Forest

The boreal forest accounts for about one-third of the world's forested area, at *c.* 2.6 x 10^6 km^2 it makes up *c.*30% of mainland Canada. It is a broad circumpolar band that extends throughout Canada, Alaska, Russia and Scandinavia. The boreal forest is home to about one-half to two-thirds of Canadas major insect taxa, consisting of *c.* 22 000 insect species (Danks and Foottit 1989). The boreal forest canopy is made up of predominately coniferous trees, but in some areas there is a large deciduous component. These two types of trees coexist is known as the boreal mixedwood forest. Following a major disturbance (*e.g.*, fire, disease, insect outbreaks) in the boreal mixedwood forest, fast growing deciduous trees are the first to return to the landscape (Rowe 1994). As deciduous trees grow and self thin to form the canopy, more slowly growing coniferous trees begin to come up in the understory. This new coniferous cohort eventually grows and replaces the canopy deciduous trees creating first a mixedwood and eventually a coniferous forest. Although natural disturbances play a major role in structuring mixedwood landscapes spatially and temporally, these are quickly being replaced by harvesting as the major disturbance in shaping boreal mixedwood forests.

1.2 Ecological role of natural disturbances

Natural disturbances are relatively discrete events in time that affect the physical environment and biological structure of ecosystems (Pickett and White 1985). In boreal forests, natural disturbances such as insect and disease outbreaks, but especially wildfire, each operating on a variety of spatial scales, are the driving forces influencing landscape structure and ecosystem processes. Large disturbance events alter forest landscapes which shifts mosaics of forest polygons varying in age structure, size, composition and dispersion (Hunter 1993, Kaila et al. 1994).

Wildfire, in particular, is a major driver of disturbance regimes in North American boreal forests (Johnson 1992, Payette 1992). In the last 150 years there has been a decrease in fire frequency, with a punctuated change in 1945 (Johnson et al. 1999), about the time that active fire suppression techniques began. This resulted in forests with over 3 times the normal fuel loads (Clark 1990), that may now be resulting in larger and more severe fires. As fire suppression efforts become more effective and forest harvest increases, harvesting is now becoming the largest disturbance on many boreal North American landscapes and historical fire patterns are rapidly changing. The ecological ramifications of this shift have yet to be fully ascertained. Harvesting affects structural and ecological features of the forest differently than fire. Some of the differences are obvious and some of them are subtle and poorly understood.

The biological assemblages that characterize boreal forests must be adapted to natural disturbance events that are fairly regular in space and time and periodically set back succession (Holliday 1991, Muona and Rutanen 1994). As a result, burned forests support a unique insect fauna. Although many species that occur in burned forests are generally favored by disturbance and also occur in other open habitat forests (Holliday 1991, Kaila et al. 1997), there are numerous insect species that are restricted to burned habitats for one or a few generations following fire (Evans 1971, Wikars 1992). Insects are thought to be attracted to burns because they are adapted to the warmer microclimate or reduced competition (Holliday 1991), the substrates created by fire are necessary for some part of the insect's life-cycle (Danks and Foottit 1989) or they feed on fire-adapted fungi growing in burned wood (Muona and Rutanen 1994). Little is known about the exact role of these 'pyrophilous' species, but it is thought that they might be involved in forest succession or alter the unique habitat created by fire to allow successful recovery of the forest (Hammond et al. 2001, Siitonen 2001). As a result, the conservation of these insects could be crucial to maintaining natural processes in disturbed forests.

Beetles have been the particular focus of numerous studies looking at the effects of wildfire. Studies on epigaeic (ground dwelling) beetles (Richardson and Holliday 1982, Holliday 1984, 1991, 1992, Wikars 1992, 1995, 1997, Wikars and Schimmel 2001, Wikars 2002) have shown that numerous species are closely associated with fire and that there is a distinct change in the beetle assemblage following fire. Additionally, Gandhi et al. (2001) found that subalpine forest patches left following fire were typically older than the surrounding forest indicating they have been skipped by fire multiple times. The unique properties of these unburned 'fire skips' supported an assemblage of epigaeic beetles different from the surrounding burned forest and undisturbed forest. Studies of saproxylic beetles (Wikars 1992, Muona and Rutanen 1994, Wikars 1997) have also identified numerous species, including bark beetles, predators, and species associated with fungi, that are attracted to recently burned forests.

Another major structural and ecological difference between wildfire and forest harvesting is the amount of coarse woody debris (CWD) left on the landscape. Numerous studies have described CWD dynamics in natural forests between disturbances (e.g. Sprugel 1984, Agee and Huff 1986, Spies et al. 1988, Lee et al. 1997, Duvall and Grigal 1999). CWD dynamics generally begin with a large input of CWD from disturbances. Then as that CWD decomposes, the lowest amounts of CWD are reached in mid-successional forests. CWD by tree mortality increases as trees die initially because of competition and thinning and later by exogenous disturbances creating elevated levels of CWD in late successional forests. Comparing these studies to those about CWD dynamics in harvested forests, Siitonen et al.(2000) found a ten fold decrease in the amount of CWD in managed forests compared to old-growth forests, with a much larger decrease in large diameter CWD than smaller diameter CWD. Furthermore, Angelstam (1997) found that CWD levels decreased 80% after a single harvest rotation, and such CWD decreases result in a decrease in the abundance of rare saproxylic species (Siitonen and Martikainen 1994).

1.3 Saproxylic insect assemblages

Speight (1989) was among the first to call specific attention to species in dead wood, and defined 'saproxylic' organisms as those that depend, during some part of the life cycle, upon dead wood, wood-inhabiting fungi or the presence of other saproxylic organisms. Decomposition of CWD with the aid of numerous saproxylic organisms is an extremely important process of nutrient cycling in the boreal forest (Harmon et al. 1986, Franklin et al. 1987, Harmon and Hua 1991). CWD provides a large variety of microhabitats for many species of arthropods (Esseen et al. 1992, Siitonen 1994a, b, Siitonen and Martikainen 1994, Ahnlund 1996, Oekland et al. 1996, Siitonen et al. 1996, Esseen et al. 1997, Hammond 1997, Kaila et al. 1997, Jonsell et al. 1998, Bakke 1999, Andersen et al. 2000, Eriksson 2000, Gerell 2000, Molino-Olmedo 2000, Schiegg 2000, Siitonen et al. 2000, Siitonen and Saaristo 2000, Ehnström 2001, Hammond et al. 2001, Jonsell and Eriksson 2001, Martikainen 2001, Siitonen 2001, Simila et al. 2002, Jonsell and Weslien 2003, Simila et al. 2003, Hammond et al. 2004), vertebrates (Bunnell et al. 1999, Bowman et al. 2000, Butts and McComb 2000), cryptograms (Kruys and Jonsson 1999), fungi (Amaranthus et al. 1994, Norden et al. 2002) and herbaceous plants (McCullough 1948, Falinski 1978).

Siitonen (2001) summarized the main factors affecting saproxylic organisms in CWD as: 1) species of CWD; 2) stage of decay; 3) species of fungi and other saproxylic species in the CWD; 4) diameter of CWD; 5) type of CWD (snags or logs); 6) amount of surrounding CWD and 7) the part of the tree the CWD originated from (*i.e.*, branches, trunk, bole, roots, *etc.*). As the tree decomposes there is a succession of organisms that inhabit the CWD (Siitonen 2001) and many of these rely on the previous occupants of the CWD to facilitate their own colonization. Given the importance of CWD to so many organisms and the key role it plays in nutrient-cycling, it has been suggested that CWD should be the primary focus of current forest management plans (Franklin et al. 1997, Lee et al. 1997, Hagan and Grove 1999).

Saproxylic organisms have been poorly studied in North America. Studies in Europe have found that centuries of intensive forest harvest have resulted in a biologically significant drop in saproxylic organisms (Siitonen and Martikainen 1994). Many of these effects can be detected in Europe because the fauna is well described and documented.

There is a need in North America to learn more about these organisms in their natural state and determine what factors affect saproxylic communities. It is important to first understand the North American fauna and how it is associated with forest habitats and other aspects of natural variation before we can accurately assess the potential impacts of industrial forestry. In North America we are able to study these organisms in relatively undisturbed forests, and perhaps better understand their primeval condition, relative to European forests. An increased understanding of the natural variation in CWD and its resident biota, and an assessment of how habitats and species respond to natural disturbances will support the design of better management practices that reduce the imprint of harvesting. These changes can be applied under an adaptive management philosophy, such as is increasingly being adopted by forest managers as a means to balancing environmental, economic and social management objectives and achieving sustainability.

1.4 Adaptive Forest Management

The realization that fire (and other natural disturbances) and traditional clear cut harvesting leave different structure and patterns on the landscape that will likely have different long-term ecological effects has prompted the science community and forest managers to explore alternative management strategies that may better approximate the ecological roles of fire in forests. This has led to the adoption of a natural disturbance paradigm (NDP) to help retain the temporal and spatial patterns created by natural disturbances within harvested landscapes (Thompson and Welsh 1993). It is hypothesized that by harvesting trees to produce landscape-level patterns similar to those produced by wildfire, ecosystem processes and function will be maintained (Hunter 1993). By employing such variable retention (VR) harvesting, and leaving residual forest structure, including standing and fallen CWD, live trees and undergrowth, on harvested blocks, it is anticipated that these residuals will act as biotic 'store-houses', ecologically equivalent to residuals left in the wake of wild-fire (Clayquot Scientific Panel 1995). The structural complexity left after a disturbance is thought to play important roles in ecosystem function and biological diversity (Bunnell et al. 1999). This structure can either be dispersed across the landscape or aggregated into clumps. VR harvesting will also affect the CWD succession by increasing the long-term input into these systems. Although this increase in the input of CWD should benefit saproxylic communities in the long term, the short term effects of variable retention harvesting are largely unknown.

Although the NDP has been widely adopted as a management philosophy, and VR harvesting is increasingly being applied as a means of implementation, there are few empirical studies to test the underlying tenets of the NDP or to identify optimal VR prescriptions that achieve a desired balance among environmental, economic and social objectives. One of the most comprehensive and well integrated studies to address these issues is the EMEND experiment (Ecological Management by Emulating Natural Disturbance). This experiment is a large-scale forest manipulation study that attempts to link harvest methods to forest regeneration procedures to promote holistic and ecologically-sensitive silviculture. The objectives of the EMEND project are: 1) to determine which forest harvest and regenerative practices best maintain biotic communities, spatial patterns of forest structure, functional ecosystem integrity in comparison with mixed-wood landscapes that have originated through wildfire and other inherent natural disturbances; and 2) to employ economic and social analyses to evaluate these practices in terms of economical viability, sustainability and social acceptability.

EMEND is located in the Clear Hills Upland, Lower Foothills ecoregion of northern Alberta, approximately 90km north-west of Peace River (56° 46' 13"N, 118° 22' 28"W). The elevation on the site ranges from 677m to 880m, and the soils at the site are fine-textured Lacustran (Work et al. 2004). The stands included in this study were 80 to 140 years old and forests in this area had never before been harvested commercially.

The EMEND project has a 2 factorial design, with one factor being cover type and the other being treatment. There are four major cover types being examined at the EMEND project based on the relative proportion of deciduous and coniferous tree species in the canopy and were chosen to represent the range of boreal mixedwood stands seen during succession (Fig. 1-1). The early successional deciduous dominated (DDOM) sites consisted of greater than 70% deciduous species, represented primarily by trembling aspen (*Populus tremuloides* Michaux) and balsam poplar (*Populus balsamifera* L.), with a small portion of paper birch (*Betula papyrifera* Marshall). Early mid-successional stands were deciduous dominated stands with a developing coniferous understory (DDOMU) reaching at least 50% of canopy height. Late mid-successional stands were mixedwood stands (MX) composed of 35%-65% of both deciduous and coniferous species in the canopy. Late successional coniferous stands (CDOM) were stands with greater than 70% coniferous species represented by white spruce (*Picea glauca (*Moench) Voss), with a small portion of black spruce (*Picea mariana* (Miller)) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm).

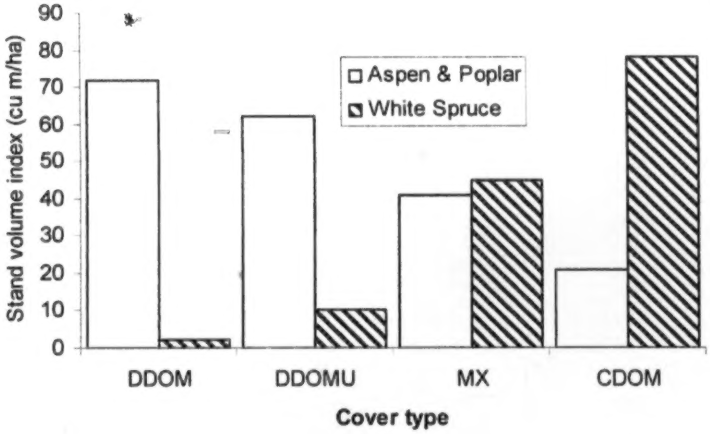

Figure 1-1 The relative abundance of canopy trees in each of the cover types: DDOM, deciduous dominated; DDOMU, deciduous dominated with a developing coniferous understory; MX, mixedwood, and CDOM, coniferous dominated.

In each of the four cover types harvesting and fire treatments have been laid out in 10ha blocks with 3 replicates of every 'cover type'-'treatment' combination across the project (except where noted) (Table 1-1). In addition to the controls there are 5 levels of VR harvesting treatments and 2 burn treatments. In the winter of 1998/1999, five VR harvesting treatments were applied to the sites using a uniform shelterwood system as follows: 1) 75% residual - 5m wide machine corridors spaced 20m (center-center) apart, leaving 15m wide retention corridors; 2) 50% residual, additional trees were removed from the retention corridors at a ratio of 1:3 (removed: leave standing); 3) 20% residual, trees were removed from the retention corridors at a ratio of 3:4; 4) 10% residual, trees were removed from the retention corridors at a ratio of 7:8, and 5) 1-2% retention, standard clearcut (see Work et al. 2004). In the 75%, 50%, 20% and 10% retention treatments all machinery was restricted to the machine corridors to avoid compaction of the soil in the retention corridors.

Table 1-1 Experimental design of the EMEND project indicating the number of replicates of each cover type treatment combination.

	Cover type			
	DDOM	DDOMU	MX	CDOM
Controls	3	3	3	3
Harvesting treatment				
1-2 % residual	3	3	3	3
10% residual	3	3	3	3
20% residual	3	3	3	3
50% residual	3	3	3	3
75% residual	3	3	3	3
Fire treatments				
Standing timber burn[a]	1			2[b]
Slash burn	3	3	3	3

[a] original plan was to have three replicates of each, but was not possible due to weather conditions.

[b] first CDOM burn was in July 1999, the second in July 2004

Fire treatments include both standing timber burns and slash burns. The standing timber burns have been difficult to do, due to environmental conditions. In the first five years only a single CDOM prescribed burn has occurred that can adequately reflect the effects of natural fire. Other attempts of burning have produced light burns that have consumed very little of the litter on the forest floor. Due to complications with the standing timber burns, additional treatments were added to the EMEND experiment. These are 10ha 'slash burn' compartments. These were commercially harvested to a 10% retention level and the resulting slash was spread throughout the block in the winter of 2002/2003. Half of each block was subsequently burned in the summer of 2003 in all cover types except the DDOM. The DDOM cover type is planned to be burned in the fall of 2004. For the studies in this thesis, I utilized the controls from all cover types (Chapter 2), the standing timber burn from July 1999 (Chapter 3) and the controls and all harvesting treatments (except 1-2% residual clearcuts) from the CDOM cover type (Chapter 4).

1.5 Objectives of this Thesis

Development of sound adaptive management requires assessment of responses of a wide range of parameters to best balance environmental and socio-economic objectives. To contribute to this larger goal I studied the structure of saproxylic (and to a lesser extent, epigaeic) beetle assemblages within the EMEND experimental template. The general objectives of this thesis are: 1) document the diversity of saproxylic beetles in a representative North American boreal mixedwood forest, 2) investigate which features in undisturbed forests influence saproxylic beetle assemblages, 3) study the effect of fire on epigaeic and saproxylic beetle assemblages and 4) determine the short term impacts of variable retention harvesting on saproxylic beetle assemblages. All objectives are based on beetles associated with still standing CWD often referred to as snags, with the addition of a ground-level component in the fire study. Throughout all aspects of this thesis CWD is the focus. In all studies, traps were placed on trees killed by girdling and on naturally dead trees to determine the effects of the age of CWD. Furthermore, CWD plots were established in 5m radii around each trap to examine the influence of nearby CWD.

Chapter Two focuses on saproxylic insects in undisturbed stands from forest types representing the typical boreal mixedwood successional pathway. Data about beetles and numerous environmental features collected from these stands shed light on their relationships in these stands. Chapter Three focuses on the distribution of epigaeic and saproxylic beetles in a prescribed burn. The burn was divided into areas based subjectively on severity of the fire, 1) fire 'skips' (unburned areas), 2) light burn and 3) severe burn. Special emphasis was given to pyrophilous beetles (*i.e.*, those that were abundant in the burned areas and not found in other treatments/areas on the rest of the EMEND project). Chapter Four focuses on the short term effects of variable retention harvesting on saproxylic insects. Five levels of harvesting retention were examined (100%, 75%, 50%, 20% and 10% retention) to determine the impacts on saproxylic beetle assemblages 1.5 and 2.5 years after harvesting. In Chapter Five, I summarize and discuss the most important results of this study and place them in a forest management context. In order to make forest harvesting more ecologically sensitive it is important to examine ecologically important groups like saproxylic beetles in undisturbed areas, areas disturbed by natural processes like wildfire and harvested areas.

Literature Cited

Agee, J. K., and M. H. Huff. 1986. Fuel succession in a western hemlock/Douglas fir forest. Canadian Journal of Forest Research **17**:697-704.

Ahnlund, H. 1996. Saproxylic insects on a Swedish dead aspen. Entomologisk Tidskrift **117**:137-144.

Amaranthus, M., J. M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research **24**:2157-2165.

Andersen, J., S. Olberg, and L. Haugen. 2000. Saproxylic beetles (Coleoptera) of Troms and western Finnmark, northern Norway with exceptional distribution in Fennoscandia. Norwegian Journal of Entomology **47**:29-40.

Angelstam, P. 1997. Landscape analysis as a tool for the scientific management of biodiversity. Ecological Bulletins **46:**140-170.

Bakke, A. 1999. High diversity of saproxylic beetles in a hemiboreal mixed forest reserve in the south of Norway. Scandinavian Journal of Forest Research **14**:199-208.

Bowman, J. C., D. Sleep, G. J. Forbes, and M. Edwards. 2000. The association of small mammals with coarse woody debris and log and stand scales. Forest Ecology and Management **129**:119-124.

Bunnell, F. L., L. L. Kremsater, and E. Wind. 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands. Environmental Reviews **7**:97-146.

Butts, S. R., and W. C. McComb. 2000. Association of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. Journal of Wildlife Management **64**:95-104.

Clark, J. S. 1990. Twentieth century climate change, fire suppression, and forest production in northwestern Minnesota. Canadian Journal of Forest Research **20**:219–232.

Clayquot Scientific Panel. 1995. Scientific panel for sustainable forest practices in Clayquot Sound, Report 5, Sustainable ecosystem management in Clayquot Sound: planning and practices. Victoria, B.C.

Danks, H. V., and R. G. Foottit. 1989. Insects of the boreal zone of Canada. Canadian Entomologist **121**:625-690.

Duvall, M. D., and D. F. Grigal. 1999. Effects of timber harvesting on coarse woody debris on red pine forests across the Great Lake states, U.S.A. Canadian Journal of Forest Research **29**:1926-1934.

Ehnström, B. 2001. Leaving dead wood for insects in boreal forests - suggestions for the future. Scandinavian Journal of Forest Research **16**:91-98.

Eriksson, P. 2000. Long term variation in population densities of saproxylic Coleoptera species at the river of Dalaelven, Sweden. Entomologisk Tidskrift **3**:119-135.

Esseen, P. A., B. Ehnström, L. Ericson, and K. Sjöberg. 1992. Boreal forests the focal habitats of Fennoscandia. Elsevier Applied Science, London.

Esseen, P. A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal Forests. Ecological Bulletin **46**:16-47.

Evans, W. G. 1971. The attraction of insects to forest fires. *in* Proceedings of the Tall Timbers Research Station, Tallahasse, Fl.

Falinski, J. B. 1978. Uprooted trees, their distribution and influences in the primeval forest biotope. Vegetatio **38**:175-183.

Franklin, J. F., D. A. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Island Press, Washington, D.C.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. Bioscience **37**:550-556.

Gandhi, K. J. K., J. R. Spence, D. W. Langor, and L. E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera : Carabidae and Staphylinidae). Biological Conservation **102**:131-141.

Gerell, R. 2000. The importance of avenues for threatened saproxylic beetles. Entomologisk Tidskrift **121**:59-66.

Hagan, J. M., and S. L. Grove. 1999. Coarse woody debris. Journal of Forestry **97**:6-11.

Hammond, H. E., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research **31**:1175-1183.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. Canadian Entomologist **129**:1009-1033.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research **34**:1-19.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. J. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133-302.

Harmon, M. E., and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems: comparing a deciduous forest in China and a conifer forest in Oregon. Bioscience **41**:604-610.

Holliday, N. J. 1984. Carabid beetles (Coleoptera, Carabidae) from a burned spruce forest (*Picea* Spp). Canadian Entomologist **116**:919-922.

Holliday, N. J. 1991. Species responses of carabid beetles (Coleoptera, Carabidae) during postfire regeneration of boreal forest. Canadian Entomologist **123**:1369-1389.

Holliday, N. J. 1992. The carabid fauna (Coleoptera, Carabidae) during postfire regeneration of boreal forest - properties and dynamics of species assemblages. Canadian Journal of Zoology **70**:440-452.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation **65**:115-120.

Johnson, E. A. 1992. Fire and vegetation dynamics—studies from the North American boreal forest. Cambridge University Press, Cambridge, U.K.

Johnson, E. A., K. Miyanishi, and N. O'Brien. 1999. Long-term reconstruction of the fire season in the mixedwood boreal forest of Western Canada. Canadian Journal of Botany **77**:1185-1188.

Jonsell, M., and P. Eriksson. 2001. A comparison of the saproxylic beetle fauna on spruce wood and birch high-stumps between the Batfors forest reserve and its surroundings. Entomologisk Tidskrift **122**:107-122.

Jonsell, M., and J. Weslien. 2003. Felled or standing retained wood--it makes a difference for saproxylic beetles. Forest Ecology and Management **175**:1-3.

Jonsell, M., J. Weslien, and B. Ehnstrom. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation **7**:749-764.

Kaila, L., P. Martikainen, and P. Punttila. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation **6**:1-18.

Kaila, L., P. Martikainen, P. Punttila, and E. Yakovlev. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. Annales Zoologici Fennici **31**:97-107.

Kruys, N., and B. G. Jonsson. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research **29**:1295-1299.

Lee, P. C., S. Crites, M. Nietfeld, H. V. Nguyen, and J. B. Stelfox. 1997. Characteristics and origins of deadwood material in aspen dominated boreal forests. Ecological Applications **7**:691-701.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletin **49**:205-218.

McCullough, H. A. 1948. Plant succession on fallen logs in a virgin spruce-fir forest. Ecology **29**:508-513.

Molino-Olmedo, F. 2000. Significance of wood for conservation of saproxylic coleoptera from Andalusia (South Iberian Peninsula). Elytron **14**:69-82.

Muona, J., and I. Rutanen. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forests. Annales Zoologici Fennici **31**:109-121.

Norden, B., T. Appelqvist, and B. Olausson. 2002. Diversity, ecology and conservation of wood-inhabiting ascomycetes in Sweden. Svensk Botanisk Tidskrift **96**:139-148.

Oekland, B., A. Bakke, S. Haagvar, and T. Kvamme. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation **5**:75-100.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In A systems analysis of the boreal forest. Cambridge University Press, Cambridge, U.K.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Richardson, R. J., and N. J. Holliday. 1982. Occurrence of Carabid Beetles (Coleoptera, Carabidae) in a Boreal Forest Damaged by Fire. Canadian Entomologist **114**:509-514.

Rowe, J. S. 1994. A New Paradigm for Forestry. **70**:565-568.

Schiegg, K. 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience **7**:290-298.

Siitonen, J. 1994a. Decaying wood and saproxylic Coleoptera in 2 old spruce forests - a comparison based on 2 sampling methods. Annales Zoologici Fennici **31**:89-95.

Siitonen, J. 1994b. Decaying wood and saproxylic Coleoptera in two old spruce forests: A comparison based on two sampling methods. Annales Zoologici Fennici **31**:89-95.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins **49**:11-41.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russion Karelia. Scandinavian Journal of Forest Research **9**:185-191.

Siitonen, J., P. Martikainen, L. Kaila, I. Mannerkoski, P. Rassi, and I. Rutanen. 1996. New faunistic records of threatened saproxylic Coleoptera, Diptera, Heteroptera, Homoptera and Lepidoptera from the Republic of Karelia, Russia. Entomologica Fennica **7**:69-76.

Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management **128**:211-225.

Siitonen, J., and L. Saaristo. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. Biological Conservation **94**:211-220.

Simila, M., J. Kouki, and P. Martikainen. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management **174**:1-3.

Simila, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation **106**:19-27.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in douglas-fir forests of western Oregon and Washington. Ecology **69**:1689-1702.

Sprugel, D. 1984. Changes in biomass components through stand development in wave-generated balsam fir forests. Canadian Journal of Forest Research **15**:269-278.

Thompson, I. D., and D. A. Welsh. 1993. Integrated resource-management in boreal forest ecosystems - impediments and solutions. Forestry Chronicle **69**:32-39.

Wikars, L. O. 1992. Forest fires and insects. Entomologisk Tidskrift **113**:1-11.

Wikars, L. O. 1995. Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera:Carabidae). Annales Zoologici Fennici **32**:375-384.

Wikars, L. O. 1997. Pyrophilous insects in Orsa Finnmark, central Sweden: biology, distribution, and conservation. Entomologisk Tidskrift **118**:155-169.

Wikars, L. O. 2002. Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation **6**:1-12.

Wikars, L. O., and J. Schimmel. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. Forest Ecology and Management **141**:189-200.

Work, T. T., D. P. Shorthouse, J. R. Spence, W. J. A. Volney, and D. W. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research **34**:417-430.

Chapter 2 Stand structure and composition, dead wood quality and saproxylic beetles

Introduction

Large and diverse assemblages of organisms are associated with coarse woody debris (CWD) in the boreal forest. These organisms use CWD for food, shelter, foraging or reproductive activities (Hammond 1997, Siitonen 2001, Hammond et al. 2004). Speight (1989) called specific attention to this community and defined 'saproxylic' organisms as those that are associated, during some part of the life cycle, upon dead wood, wood-inhabiting fungi or the presence of other saproxylic organisms. Saproxylic organisms play Esseential ecosystem roles in relation to decomposition and nutrient cycling (Reichle 1977, McGill and Spence 1985, Hammond 1997, Hammond et al. 2001). Although the functional roles of saproxylic organisms depend on associations with a large fungal component, insects, particularly beetles, comprise a large part of the biodiversity associated with dead wood and they have become the focus of many studies in Europe (Siitonen and Martikainen 1994, Martikainen et al. 2000, Martikainen 2001, Siitonen 2001, Simila et al. 2002, Sippola et al. 2002) and are receiving increasingly more attention in North America (Hammond 1997, Hammond et al. 2001, Hammond et al. 2004).

Saproxylic organisms, especially rare and threatened species, are sensitive to anthropogenic disturbances, and industrial forestry has resulted in biologically significant declines in diversity and even local extirpation of some European species (Siitonen and Martikainen 1994). These negative effects can be detected in Europe because the fauna is well described. It is important to first understand the North American fauna and how it is associated with forest habitats and other aspects of natural variation before we can accurately assess the impacts of industrial forestry. Furthermore, in North America we are able to study these organisms in relatively undisturbed forests, and perhaps understand their primeval condition relative to European forests.

Many factors may affect saproxylic beetle assemblages in the boreal mixedwood forest of northern Alberta. However, it is now widely recognized that both quantity and quality of CWD is central to maintaining the diversity of insects, cryptograms and fungi in the boreal forests (Esseen et al. 1997, Ehnström 2001). Another factor that may affect saproxylic beetle communities is the relative abundance of the various canopy trees making up a forest (Siitonen 2001). This feature can be generally related to succession in the boreal mixedwood forest, as stands with relatively more deciduous trees in the canopy represent earlier successional stages, closer in time to the most recent disturbance event (Rowe 1994). Alternatively coniferous trees begin to dominate the canopy in older stands, or further in time from the most recent disturbance event.

Hammond (1997), and Hammond et al. (2001, 2004) have studied the saproxylic fauna of aspen dominated stands in the boreal mixedwood forests of Alberta and reviewed methods used to collect saproxylic insects. This work demonstrated that type of CWD is important to insects and that there is a distinct succession of insects during the breakdown of CWD in early successional stands. In contrast, boreal coniferous and mixedwood stands have received little attention in North America. In this chapter, I compare saproxylic beetle communities in undisturbed stands spanning the canopy tree succession gradient from deciduous dominated stands to coniferous dominated stands. Additionally, I assess the impact of quality and quantity of CWD on saproxylic beetle assemblages. My goal is to lay a foundation for detecting the impacts of natural and anthropogenic disturbances on this sensitive forest community in western Canada.

Materials and Methods

Study Sites. The field aspects of this study were conducted at the Ecosystem Management by Emulating Natural Disturbance (EMEND) research site. EMEND is located in the Clear Hills Upland, Lower Foothills ecoregion of northern Alberta, approximately 90km north-west of Peace River (56° 46' 13"N, 118° 22' 28"W). The elevation on the site ranges from 677m to 880m, and the soils at the site are fine-textured lacustrian (Work et al. 2004).

The sites used for this study were located in three replicate, untreated stands of at least 10ha in size representing each of four cover types. Cover types were based on the relative proportion of deciduous and coniferous tree species in the canopy and were chosen to represent the range of boreal mixedwood stands seen during succession (Fig. 2-1). The early successional deciduous dominated (DDOM) sites consisted of greater than 70% deciduous species, represented primarily by trembling aspen (*Populus tremuloides* Michaux) and balsam poplar (*Populus balsamifera* L.), with a small portion of paper birch (*Betula papyrifera* Marshall). Early mid-successional stands were deciduous dominated stands with a developing coniferous understory (DDOMU) reaching at least 50% of canopy height. Late mid-successional stands were mixedwood stands (MX) composed of 35%-65% of both deciduous and coniferous species in the canopy. Late successional coniferous stands (CDOM) were stands with greater than 70% coniferous species represented by white spruce (*Picea glauca* (Moench) Voss), with a small portion of black spruce (*Picea mariana* (Miller)) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm).

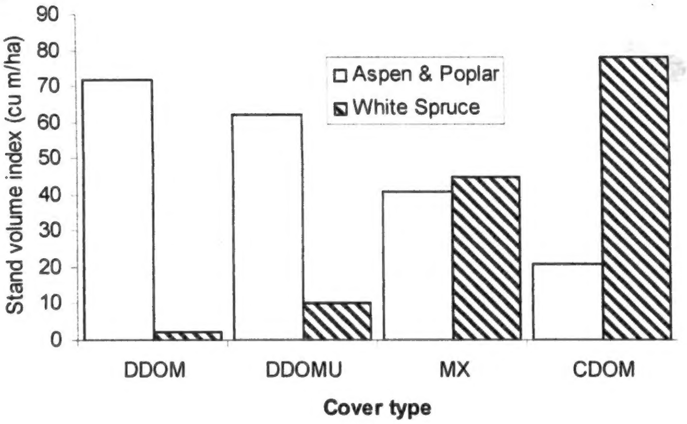

Figure 2-1 The relative abundance of canopy trees in each of the cover types: DDOM, deciduous dominated; DDOMU, deciduous dominated with a developing coniferous understory; MX, mixedwood, and CDOM; coniferous dominated.

Sampling Methods and Identification. Saproxylic beetles were sampled with passive barrier (window) traps, similar to those deployed by Hammond (1997), as modified from Käila (1993). Traps consisted of a clear piece of plastic (plexiglass®), 1.5mm x 20cm x 30cm attached perpendicularly to trees to intercept insects on or near the tree. Insects then passed through a cloth funnel attached to the bottom of the interception panel, and were collected in a small plastic bag filled with ethylene glycol at the bottom of the funnel. This plastic bag was replaced with a new bag of fresh ethylene glycol every 2-3 weeks throughout the sampling period. Passive barrier traps were chosen as they are an unbiased sampling method for flying arthropods orienting to trees, snags and logs and they are easy to replicate in quantity. This method provides large data sets suitable for community level statistical analysis. The main drawback of such sampling is identifying the saproxylic taxa. This depends on the natural history information and taxonomic keys available for particular species.

All traps were deployed in April 1999. Three sampling sites were selected at random locations in each of the three replicated stands of each canopy compositional type (cover type). Randomized grid points were used to select the first site in each stand and the other two sites were established successively at a random distance and bearing from the previously-established site. Two traps were deployed at each site on the dominant tree species, *P. tremuloides* in the DDOM and DDOMU cover type and *P. glauca* in the CDOM cover type. The sampling effort was doubled in mixedwood cover types with one set of traps placed on *P. tremuloides* and another on *P. glauca*. Catches from the mixedwood stand have been treated as two stand level treatments throughout the analysis and are designated as 'MX-aspen' when referring to traps on the deciduous species and 'MX-spruce' when referring to traps on the coniferous species. In total, 90 traps were deployed.

One trap at each site was placed on a naturally dead tree (snag) estimated to have died in the last 2-5 years based on physical characteristics (all foliage dropped, but most bark and small branches retained). The second trap was placed at least 15m and no greater than 50m away from the snag on a tree of similar diameter that had been girdled in April 1999. We aimed to kill trees by girdling using a hatchet to cut a band at least three inches wide to the depth of the sapwood at a height of approximately 50cm. All traps were placed on their respective trees at approximately breast height. Sampling started in April and continued until September for three years (1999-2001). Samples were collected every 2 to 3 weeks and initially stored in ethylene glycol until the beetles could be removed from the samples, and then transferred to 70% ethanol for storage.

All beetles were identified in the laboratory to the lowest taxonomic level possible using current literature and local expertise. In most cases, species-level identification was possible except for the Aleocharinae (Staphylinidae), and some genera in the Nitidulidae, Lathridiidae and Leiodidae. Beetles were classified as saproxylic based on the definition by Speight (1989). Family and generic nomenclature followed that of Arnett (2001a, 2001b) and species nomenclature followed that of Bousquet (1991). Synoptic collections of all beetles were deposited in the insect museums at the University of Alberta and the Northern Forestry Centre, Canadian Forest Service.

CWD measurements were collected both at the stand level in 1998 and local amounts around each trap in 2001. Stand level CWD was measured using 18 CWD star plots (see below) per stand during the summer of 1998. In each stand a total of six 40m transects were established. Three transects were placed near the beetle sampling sites and three additional transects were established in the same manner as the beetle sampling sites. Star plots were placed randomly along transects with a minimum of 5m between each plot. Star plots consisted of three 5m transects radiating out from a central point separated by 120°. The diameter of all pieces of woody material 7.0cm or greater was recorded along with the decay class. Decay classes were divided into three categories: 1) windfall from previous winter; 2) windfall created from previous seasons, and 3) material in advance stages of decay (losing bark and starting to rot). Stand level volume estimates were then completed using the Van Wagner formula (Van Wagner 1968). At each of the 6 CWD transects in each stand, 40m x 2m tree plots and 40m x 10m snag plots were conducted, recording the number and diameter of each species within the plots.

Local measurements of CWD consisted of measuring the diameter at breast height (DBH) for all trap trees in the middle of the second sampling year. CWD plots (5m radius) were established around each trap tree in the middle of the third sampling year. The number of pieces of CWD in each plot was counted and categorized as: 1) naturally occurring stumps (<1.5m high); 2) snags A, standing recently-dead trees, all bark was still intact, and retained many of the small branches; 3) snags B, standing dead trees, missing some bark and most of the small branches; 4) snags C, standing dead trees, missing a lot of bark, close to falling over; 5) logs A, freshly fallen logs; 6) logs B, logs at intermediate stages of decay, or 7) logs C, logs at advanced stages of decay, with conspicuous "red rot" and moss growth.

Data Analysis. Capture from each trap was standardized to catch per day to adjust for uneven sampling effort resulting from animal disturbance of some traps. All species were retained in all analyses, including rare species (those collected in only one sample). Although rare species have little impact on the community level analysis they are the species that are likely most threatened with local extinction as a result of forestry practices (Siitonen and Martikainen 1994).

The data set was divided depending on the habitat comparisons. When examining the effect of tree species, only the traps in the mixedwood habitat type were compared, when examining aspen succession, only traps on aspen trees in the DDOM, DDOMU and MX-Aspen sites were used, and when examining conifer succession, only MX-Spruce and CDOM sites were used. Results were transformed to presence-absence data for some analyses. This approach focuses the analysis on changes in species composition not changes in the catch of any particular taxa.

One-factor ANOVA was used to compare the mean DBH of trap trees among cover types and two-factor ANOVA was used to compare, stand level volumes of downed woody debris (DWD) and snags, the number of pieces of each type of CWD in the 5m radius CWD plot around each trap tree and to compare total beetle catch across cover type and tree mortality factor (natural or girdled). Analyses were performed using SPSS (2001), with cover type and CWD type as the independent variables and DBH or number of CWD pieces of each type as the dependent variable. Tukey HSD *post hoc* tests were used to compare individual cover types and CWD types.

To correct for uneven catch rates, rarefaction was used to compare species richness using EstimateS (Colwell 2000). Rarefaction is a method of estimating the number of species expected in a sub-sample drawn randomly from the larger sample (Magurran 1988). Chao2, an incidence-based estimator of species richness, was used to estimate total species richness of the entire community (Chao 1987) using EstimateS (Colwell

2000). These analyses were performed on the entire data set, before standardization, for each cover type independently.

Saproxylic beetle assemblage structure was compared among forest cover types, tree species and mortality agent using a non-metric multidimensional scaling (NMS) ordination as implemented by PCOrd (McCune and Medford 1999). Ordinations were used to determine whether groups of beetles were associated with a specific habitat. NMS ordination was chosen over other ordination techniques because it is well suited for arthropod community analysis and avoids the assumption of linear relationships among variables (Clarke 1993).

The stress in an ordination is crucial to its final configuration. NMS uses pair-wise comparisons to find the distance between all the points in the ordination. Distances are ranked from smallest to largest. The ordination solution is then plotted against the initial ranked real distance. Stress is the measure of the departure of the ordination solution from the original ranked distances or the departure from monotonicity. Clarke (1993) (adapted by McCune and Grace (2002)) interprets a stress <5 to be an excellent representation of the data with no prospect for misinterpretation, ≤ 10 as a good ordination with no real risk of drawing false inferences, and 10-20 as a possibly useful picture, although values at the upper end have the potential to mislead.

The final ordination was performed with the "slow and thorough" autopilot feature in PCOrd using the Sorensen (Bray-Curtis) distance measure. The autopilot feature uses a random number generator to generate a starting configuration and performs up to 400 iterations with this starting point until an instability criterion (standard deviation of the stress over the proceeding iterations) of 0.0001 is reached. This process is repeated for a 6-dimensional to a 1-dimensional configuration. The whole process is then repeated 40 times with real data, with different starting configurations. Fifty additional randomized runs are made shuffling the data within columns (species) between each run and using different random starting configurations. The 'best' configuration, defined as the one with the lowest stress, is then selected for each dimension. The final dimensionality of the ordination is selected when additional axis do not lower the stress by 5 or more. This final dimensionality and configuration is accepted as significant if the final stress is lower than that of 95% of the randomized runs using a Monte-Carlo test.

The axes are unique for each dimensionality of the ordination; the first axis in a 2-dimensional ordination is different than the first axis in a 3-dimensional ordination or a 1-dimensional ordination. Axes of the NMS ordinations are independent from the final arrangement of sample points produced, therefore the ordination points can be rotated without changing the total variance explained by the ordination, just the relative variance explained by each axis. The axis numbers are arbitrary, so axis 1 does not necessarily explain the majority of the variance. This is different from other ordination techniques (*i.e.*, PCA) where axis 1 is the most important and is independent whether there are 2 or 20 axes.

An overlay of species was used in many of the ordinations. Species that occupy a similar ordination space to that of samples or groups of samples can be interpreted to be closely associated with those samples. Species overlays identify beetles that are representative of beetle assemblages and habitat types.

Indicator species analysis (Dufrene and Legendre 1997) was used to detect and describe the importance of beetle species in differentiating habitat types (cover type, tree species, mortality factors). This analysis was performed using PCord (McCune and Medford 1999) which combines the relative catch and the relative frequency of a species into an indicator value between 0 (no indication) and 100 (perfect indication). Indicator values were then evaluated against a Monte-Carlo test statistic.

Structural variables were compared to species assemblages using multivariate regression trees (MRT) (De'Ath 2002). MRT have been used successfully to compare insect communities with environmental factors (Work et al. 2004). MRT is a rule-based technique creating dichotomies based on environmental variables. It is a hierarchical technique where each split is chosen to minimize the dissimilarity in the sites within the clusters. Distance measure used was Sorensen (Bray-Curtis). The tree is then "pruned" based on a stopping rule to have the smallest (or close to the smallest) mean square error (Breiman et al. 1984). The data are then presented in the form of a tree with species abundance graphs illustrating changes in species assemblages. The entire saproxylic beetle community was compared to 4 categorical variables (decay stage, tree species, stand and cover type), and 29 continuous variables (DBH, mean stand DWD, mean stand DWD by species, mean stand DWD by decay class, stand density of snags, stand density of snags by species and counts of local CWD around each trap). MRT were computed using R package (R Development Core Team 2004).

Results

Spruce trees were effectively killed by girdling within the 3-year time frame of this study, however, only a single aspen tree died as a result of girdling, despite the severity of the treatment. A total of 8187 beetles representing 46 families and 235 species were collected in the undisturbed stands at the EMEND research site. Based on natural history information in the literature (Hatch 1953a, b, c, d, e, White 1983, Arnett and Thomas 2001a, b) 7423 beetles (91% of total) representing 159 species (68%) are considered saproxylic and are included in the subsequent analyses.

Coarse Woody Debris. There were no significant differences in the volume of DWD among cover types (ANOVA, $F_{3,24}$=1.17, P=0.34) (Fig. 2-2). Overall, there was a significantly more deciduous DWD than coniferous DWD (ANOVA, $F_{2,24}$=16.48, P<0.001) and a significant interaction between cover type and DWD type (ANOVA, $F_{6,24}$=4.26, P=0.005). *Post hoc* tests revealed there was significantly more coniferous DWD in stands with a higher proportion of coniferous trees in the canopy (Fig. 2-2). The pattern is similar for the snag density data. There were significant differences in the overall density of snags among cover types (ANOVA, $F_{3,16}$=5.12, P=0.01) with the coniferous cover type having significantly more snags than the deciduous dominated cover type (P=0.01). Overall, there were significantly more deciduous snags than coniferous snags (P=0.01). There was a significant interaction between cover type and type of snag (ANOVA, $F_{3,16}$=49.55, P<0.001) with a large decrease in the number of deciduous snags in stands with a greater proportion of coniferous trees (Fig. 2-3).

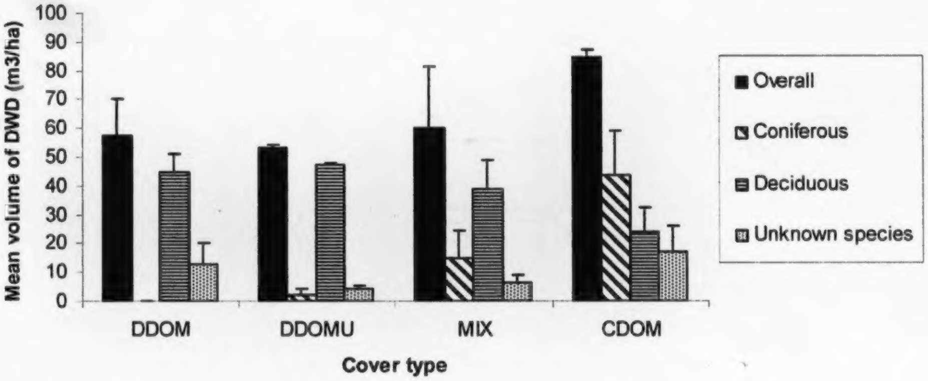

Figure 2-2 Mean volume of downed woody debris (DWD) in each cover type. Error bars represent one standard error above the mean.

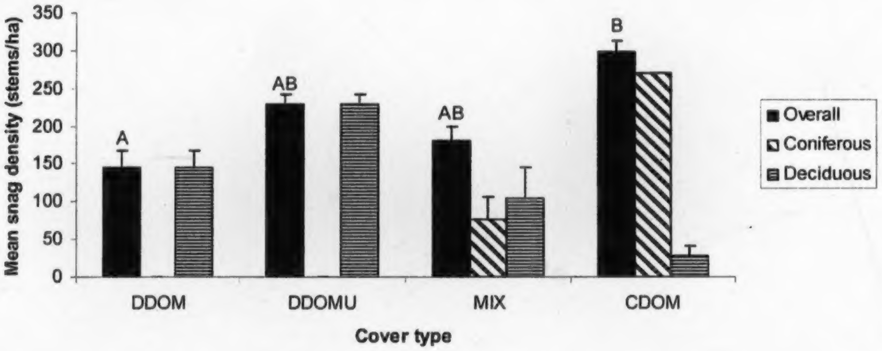

Figure 2-3 Density of snags in each cover type. Error bars represent one standard error above the mean. Letters denote differences in overall snag density among cover types.

There were no significant differences in diameter of trap trees across the five species x cover type combinations (Figure 2-4) (ANOVA, $F_{4,10}$=1.07, P=0.42).

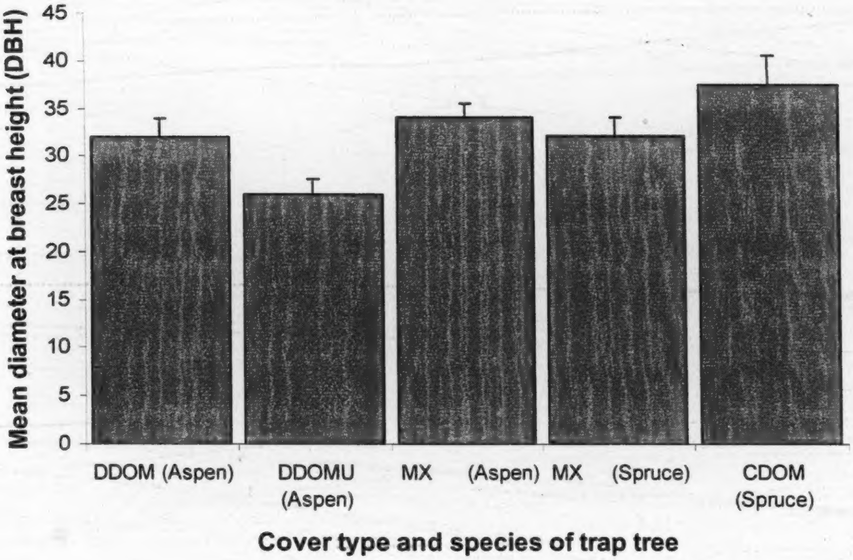

Figure 2-4 Diameter at breast height (DBH) (cm) (+ standard error) of trap trees in each cover type.

There was a complex relationship between cover type and CWD at the local scale (Fig. 2-5). In fact, both amount (ANOVA, $F_{4,70}$= 12.05, P<0.001) and type of CWD ($F_{6,70}$=36.50, P<0.001) differed among stands. Tukey's *post hoc* test indicated that DDOMU (P<0.01) and MX-Aspen (P<0.001) stands had significantly more CWD around the trap trees than any other cover type. In terms of relative amounts of CWD, over all trap sites, there were significantly more logs in later stages of decay (logsB and logsC) than any other type of CWD (Table 2-1). The significant interaction between cover type and CWD type reflected the fact that DDOMU and MX-Aspen stands had significantly more logs in mid and late stages of decay ($F_{24,70}$= 2.44, P<0.001). The general pattern is an increase in logs in intermediate (logsB) and late stages (logsC) of decay around traps in DDOM and around the traps placed on aspen trees in the mixedwood stands (MX-Aspen).

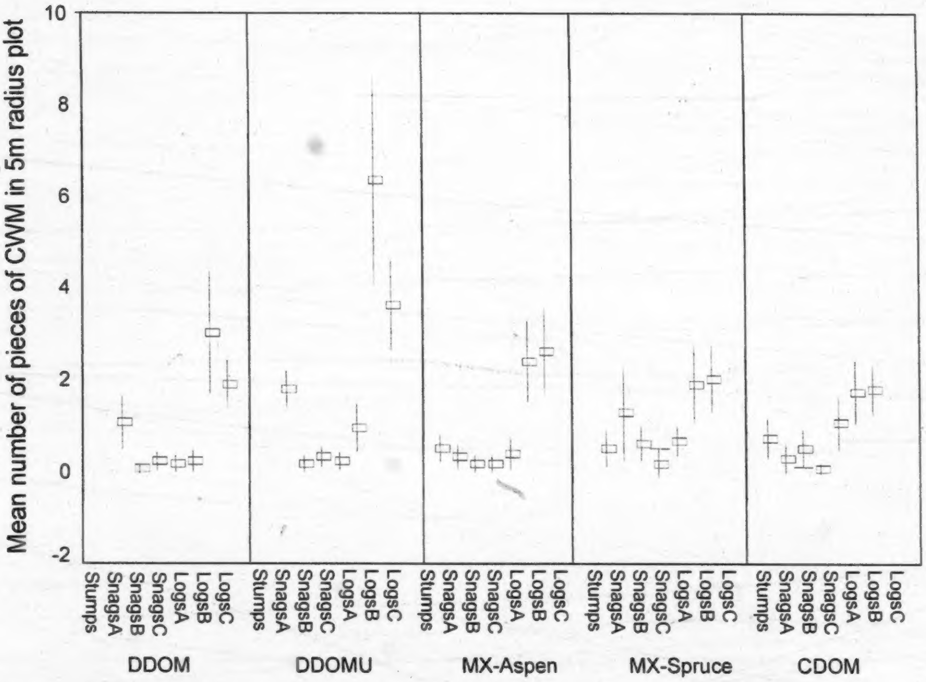

Figure 2-5 Number and type of pieces of CWD in each of the five cover types. Boxes represent mean number of CWM pieces in 5m radius plots centered on traps. Error bars represent 2 standard errors above and below the mean.

Table 2-1 P values of the Tukey's *post hoc* test on the different types of CWD across all cover types. * indicates significant differences.

	Stumps	SnagsA	SnagsB	SnagsC	LogsA	LogsB	LogsC
Mean	6.93	3.07	2.73	1.27	5.73	23.33	17.73
Stumps		0.45	0.35	0.08	1.00	0.00*	0.00*
SnagsA			1.00	0.97	0.83	0.00*	0.00*
SnagsB				0.99	0.74	0.00*	0.00*
SnagsC					0.28	0.00*	0.00*
LogsA						0.00*	0.00*
LogsB							0.08

Tree Species, Snag Quality and Saproxylic Beetles. Effects of tree species and snag quality were tested in mixedwood stands as stand background was held constant. Rarefaction estimates of saproxylic beetle species richness (Fig. 2-6) indicate that traps on aspen trees accumulated species faster than those on spruce trees, but that those on spruce trees collected many more individuals (Table 2-2). In fact, traps in the coniferous dominated stands (CDOM) collected far more individuals than did traps in any other forest cover type, and as a result, the CDOM community was more fully characterized than those from other cover types. Rarefaction estimates of species richness (Fig. 2-6) and the Choa2 estimate of total species richness (Table 2-2) indicate that only 48-69% of the total expected species in the community were sampled over the four cover types and that the CDOM community was the best characterized.

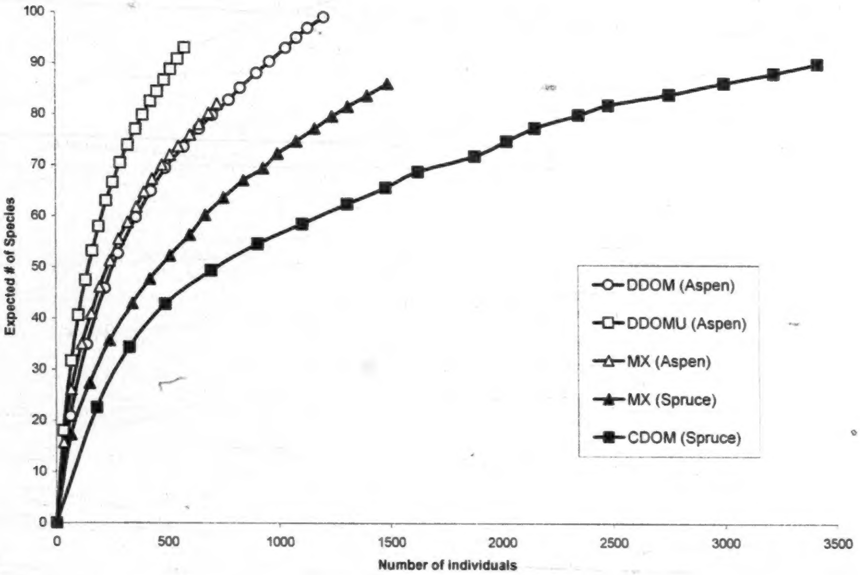

Figure 2-6 Rarefaction estimates of species in each cover type and trap tree species.

Table 2-2 Overall species richness, chao2 estimate of species richness and species catch for each cover type and tree species

Stand type	Species richness	Chao2 estimate of species richness	Total abundance
DDOM	99	143	1206
DDOMU	93	141	581
MX-Aspen	82	171	724
MX-Spruce	86	147	1492
CDOM	90	131	3420

Saproxylic beetles collected on girdled and naturally dead aspen and spruce trees in three 10ha mixedwood stands over three years consisted of 129 species, with 64 of those species occurring on both aspen and spruce trees, 32 species occurring on only aspen and 33 species occurring on only spruce trees. NMS ordination of this data set produced an ordination with a stress of 7.5, which was significantly different than randomized data based on a Monte Carlo test ($P<0.02$) (Fig. 2-7). The coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space (r^2) for axis 1 is 0.651 and axis 2 is 0.247, and the total variation explained by the ordination is 89.8%. Each sampling point on the ordination represents three traps randomly placed in a 10ha stand of trees. The resulting ordination was highly significant because of the relatively low stress and the high variance explained by the two axes. Axis 1 explains over twice as much variation as axis 2 and thus should be heavily emphasized in interpretation.

Variation associated with the two tree species more-or-less separates along axis 1 (Fig. 2-7A), with the spruce situated farthest to the right and the aspen on the left. There is a clear separation between the girdled and naturally dead spruce trees along axis 2, partially due to the fact that 4.8 times as many beetles were collected on girdled spruce trees as on naturally dead spruce trees, with catch rates of 10.23 beetles/day and 2.10 beetles/ day, respectively. There is a slight separation of traps on girdled and naturally dead aspen trees along axis 2. This ordination demonstrates distinct differences between the saproxylic beetle assemblages on aspen and spruce trees as well as difference in the assemblages on girdled and naturally dead spruce trees, and to a lesser extent differences on aspen trees.

The species overlay on the initial ordination of the mixedwood community (Fig. 2-7B) suggests that numerous species were closely associated with girdled spruce trees. A species indicator analysis (Table 2-3) of this data found 12 species indicative of differences between aspen or spruce and dead or girdled trees, 8 of which were indicative of girdled spruce. Seven of these 8 species were bark beetles and their associated predators.

Additional ordinations performed on this data set revealed no striking patterns of temporal variation in beetle activity over the three-year study.

The initial ordination had a relatively low mean stress of 7.5 indicating it is a reasonable representation of the data. Additional ordinations using only presence-absence data did not lower the stress and no additional trends were detected in these ordinations. Therefore most of the groupings in the original ordination reflect shifts in relative species abundance and not necessarily compositional differences.

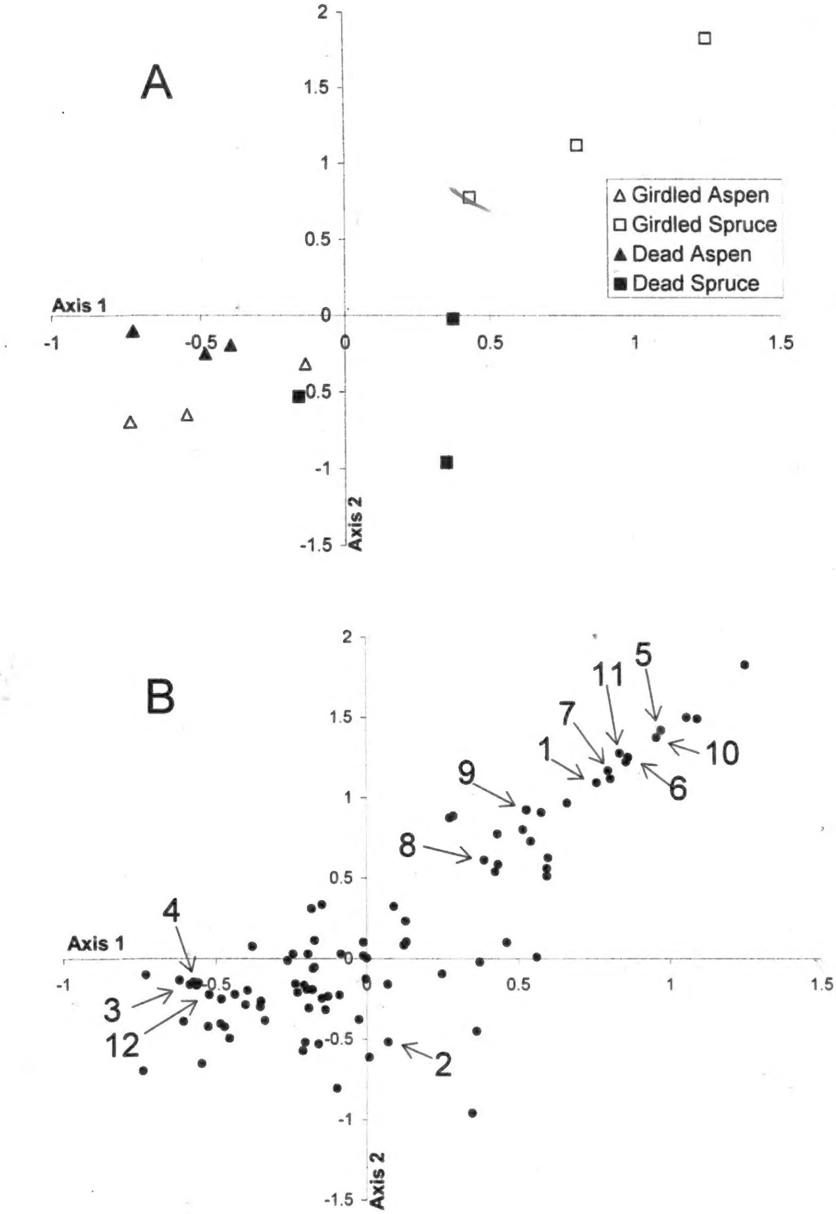

Figure 2-7 NMS ordination of 114 species and 12 sample units of aspen and spruce trees in mixedwood stands: A) samples in species space, and B) overlay of species on the initial ordination. Numbers correspond to Table 2-3, species with a significant indicator value to stand and mortality type.

Table 2-3 Significant indicators species of girdled or dead aspen or spruce trees in mixedwood stands.

Ordination number	Family	Species	Total catch (beetles/day)	Tree species	Mortality factor	Observed indicator value	Indicator value from randomized tests	
							Mean± SD	P
1	Scolytidae	*Xylechinus montanus* Blackman	0.8490	Spruce	Girdled	78.6	56.2±8.47	0.015
2	Mycetophagidae	*Mycetophagus quadriguttatus* P.W.J.Muller(+)	0.0410	Spruce	Dead	100	32.5±17.21	0.017
3	Staphylinidae	*Lordithon fungicola* Campbell	0.2065	Aspen	Dead	100	31.7±17.4	0.018
4	Cucujidae	*Cucujus clavipes puniceus* Mannerheim	0.0422	Aspen	Dead	100	30.7±17.89	0.018
5	Scolytidae	*Dryocoetes affaber* (Mannerheim)	3.7668	Spruce	Girdled	94.2	55±17.02	0.023
6	Colydiidae	*Lasconotus* complex LeConte	0.1116	Spruce	Girdled	92.3	34.2±17.6	0.023
7	Scolytidae	*Crypturgus borealis* Swaine	0.2040	Spruce	Girdled	91.2	34.2±16.78	0.023
8	Scolytidae	*Polygraphus rufipennis* (Kirby)	0.4585	Spruce	Girdled	59.3	36.8±10.03	0.023
9	Staphylinidae	*Phloeostiba lapponicus* (Zetterstedt)	0.0767	Spruce	Girdled	87.5	33.3±16.52	0.033
10	Scolytidae	*Scierus annectans* LeConte	2.1340	Spruce	Girdled	85.9	65.3±14.97	0.037
11	Rhizophagidae	*Rhizophagus dimidiatus* Mannerheim	0.3462	Spruce	Girdled	86	49.6±17.96	0.039
12	Cephaloidae	*Cephaloon tenuicorne* LeConte	0.0401	Aspen	Dead	81.8	33.9±15.15	0.046

Beetles of the deciduous cover type. Standardized catch (beetles/day) for traps on girdled and dead aspen trees in the DDOM cover type were 3.26 and 7.54, respectively, in the DDOMU were 1.91 and 3.06 and in the MX (Aspen) were 1.98 and 4.27. More beetles were collected on dead trees than on girdled trees ($F_{1,48}$=8.25, P=0.006), and the catch of beetles differed significantly across the three cover types ($F_{2,48}$=3.89, P=.027). Tukey's *post hoc* tests indicated that beetle catch was higher in DDOM stands than in DDOMU stands (P=.028) but that catch rate did not differ between DDOM and MX-Aspen stands (P=0.83). The somewhat higher catch of beetles on girdled aspen trees in DDOM reflects higher beetle captures observed on a single tree that died during the study and collected 2 to 28 times as many beetles than any other girdled aspen tree.

A total of 131 species were collected in stands when the dominant or co-dominant tree was a deciduous species. Application of NMS to these data resulted in a 3-dimensional ordination with a mean stress of 8.8 (Fig 2-8A). Axes 1,2 and 3 explain 31.3%, 26.9% and 30.1% of the variation, respectively. Each point on the ordination represents the combined catches of 3 traps in a 10ha stand of trees. The ordination (Fig. 2-8A) shows a large separation of data points between girdled and naturally dead trees along axes 2 and 3, indicating that CWD quality (time since death) was the single largest factor affecting saproxylic beetle assemblages in the deciduous dominated and co-dominated stands. The single sample from girdled trees that clustered with the dead trees was from the previously noted tree that died during the study period. Additional ordinations indicated that there was no striking additional temporal component to this data.

A species indicator analysis of these data found 16 species that discriminated between dead and girdled deciduous trees with 14 of those indicative of dead trees and only 2 indicative of girdled trees that were still living (Table 2-4). Additionally, 12 species from a variety of families were indicative of the DDOM cover type, while only 4 species indicated aspen trees in MX stands. The NMS ordination associated with presence-absence data (Fig. 2-8B) has a 3-dimensional solution with a mean stress 13.4 and was of significantly different from randomized runs using a Monte Carlo test (P<0.0196). Axes 1, 2 and 3 explain 41%, 17% and 25% of the variation, respectively. Thus the results suggest a succession in saproxylic beetle assemblages as the coniferous component in these deciduous stands increases. Stands with relatively low abundance of coniferous trees (DDOM) clustered high on axis one, the axis explaining the most variance, and stands with relatively low conifer abundance (MX-Aspen) clustered out lower on axis 1. Stands with intermediate levels of coniferous trees (DDOMU) clustered between the DDOM and MX-Aspen stands.

Table 2-4 Significant indicators species of different girdled or dead aspen trees in deciduous dominated or co-dominated cover types.

Family	Species	Total catch (beetles/day)	Cover type	Mortality factor	Observed indicator value	Indicator value from randomized tests	
						Mean± SD	P
Anobiidae	*Ptilinus lobatus* Casey	0.2058	DDOM	Dead	63.8	29.5±10.88	0.007
Sphindidae	*Odontosphindus clavicornis* Casey	0.1725	DDOM	Dead	69.7	31.2±12.67	0.008
Rhizophagidae	*Rhizophagus remotus* LeConte	0.3915	DDOM	Dead	60.9	36.7±12.3	0.008
Melandryidae	*Melandrya striata* Say	0.2007	DDOM	Dead	52.1	29.2±8.7	0.008
Lathridiidae	*Melanophthalma villosa* (Zimmermann)	1.8464	DDOM	Dead	52.1	31.7±5.82	0.008
Curculionidae	Weevil to be determined (Cur1)	0.0805	DDOM	Girdled	89.2	26.1±15.54	0.01
Elateridae	*Ctenicera resplendens* (Eschs.)	0.1392	DDOM	Girdled	54.5	28.9±10	0.013
Anobiidae	*Hemicoelus carinatus* (Say)	0.2331	DDOM	Dead	47.8	29.3±7.77	0.024
Erotylidae	*Triplax thoracica* Say	0.1693	DDOM	Dead	79.9	31±16.27	0.028
Scolytidae	*Trypodendron lineatum* (Olivier)	0..4129	MX-Aspen	Dead	71.5	38.7±14.29	0.028
Cephaloidae	*Cephaloon tenuicorne* LeConte	0.0401	MX-Aspen	Dead	81.8	27.6±14.79	0.029
Carabidae	*Platynus decentis* (Say)	1.6306	DDOM	Dead	35.9	26.7±3.99	0.029
Nitidulidae	*Glischrochilus siepmanni* W.J.Brown	0.2284	DDOM	Dead	50.4	29.5±8.81	0.031
Scolytidae	*Trypodendron retusum* (LeConte)	1.1861	DDOM	Dead	68.8	57.7±4.56	0.037
Lathridiidae	*Lathridius minutus* (Linné)	0.1789	MX-Aspen	Dead	38.7	27.8±5.9	0.037
Melandryidae	*Xylita livida* (C.R.Sahlberg)	0.0733	MX-Aspen	Dead	70.1	30±15.39	0.044

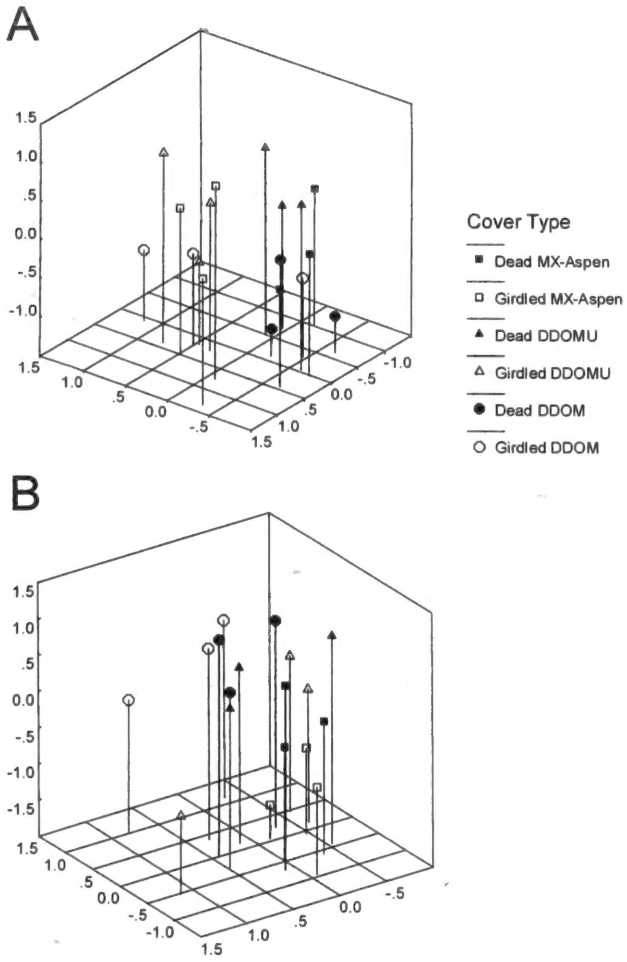

Figure 2-8 NMS ordination of 131 species and 18 samples collected from girdled and dead aspen in deciduous dominated or co-dominated stands; A) abundance data, and B) presence / absence data.

Beetles of the coniferous cover type. In stands where the dominant or co-dominant canopy tree was white spruce (CDOM, MX), traps placed on white spruce trees collected a total of 117 saproxylic beetle species over the three years of the study. The NMS ordination on abundance data (Fig. 2-9A) achieved a 2-dimensional solution with a final stress of 6.49. This solution was significantly different than that obtained from randomizations using the Monte Carlo test ($p<0.02$). Axes 1 and 2 explain 3.4% and 82.8% of the variation, respectively. All but one of the samples from conifer dominated sites clustered in the top right quadrant. In contrast, all of the dead spruce trees in mixedwood stands clustered low on axis 2. A comparison of the ordination of samples with the species overlay (Fig. 2-9B) shows that many species were specific to CDOM stands. This is supported by the species indicator analysis (Table 2-5) which found 9 species indicative of dead or girdled trees, but only in CDOM stands. Clearly there are large differences in assemblage structure between girdled and dead trees in CDOM stands and between MX and CDOM stands for dead trees.

To explore temporal changes in the saproxylic fauna of conifers, data were analyzed separately by year. NMS ordination achieved a 2-dimensional ordination with a final stress of 15.8 (Fig. 2-10). Axes 1 and 2 explain 19.2% and 57.2% of the variation. There appears to be slight but inconsistent groupings of the beetle fauna by cover type along axis 1 (Fig. 2-10A) and tree mortality along axis 2 (Fig. 2-10B). Axis 2 explains most of the variance and samples appear to be distributed by year along axis 2 (Fig. 2-10C), with most of the year 1 samples clustering below axis 1 and most of the year 3 samples clustering above axis 1. The spread of species along axis 2 appears to describe yearly differences in beetle assemblages (Fig. 2-10D). Overall it appears that there was a high degree of succession of beetle assemblages over the three years of the study.

Species indicator analysis was used to compare differences in saproxylic beetle assemblages over the three years of the study. Ten species, mostly bark beetles and their predators, were significant indicators of girdled trees in year 3 (Table 2-6) but, interestingly, none were indicators for year 1 and year 2 assemblages. In contrast, indicator analysis on naturally dead trees found only 2 species to be indicative of year 3 (Table 2-6) and one species indicative of year one. The species indicator analysis shows that the greatest changes in species assemblages occurred in the third year on girdled trees.

The differences in saproxylic beetle assemblages in girdled and dead trees are illustrated in Fig. 2-11. There was a large increase in catch of beetles, particularly bark beetles (Scolytidae) on girdled trees in the coniferous dominated and mixedwood cover types during the first three years after girdling. The response is stronger for coniferous trees, which were killed quickly by girdling, than in the aspen trees, most of which managed to live for 3 years after being girdled.

Bark beetles and their predators were consistently significant indicators of coniferous stands and trees (Table 2-3, 2-5, 2-6). Almost all other insects identified as indicators where fungivores and predators. The analyses indicated that saproxylic beetle assemblages are sensitive to CWD quality (tree species and time since death) and to changes in relative abundance of canopy trees, especially in the late successional conifer dominated and co-dominated stands.

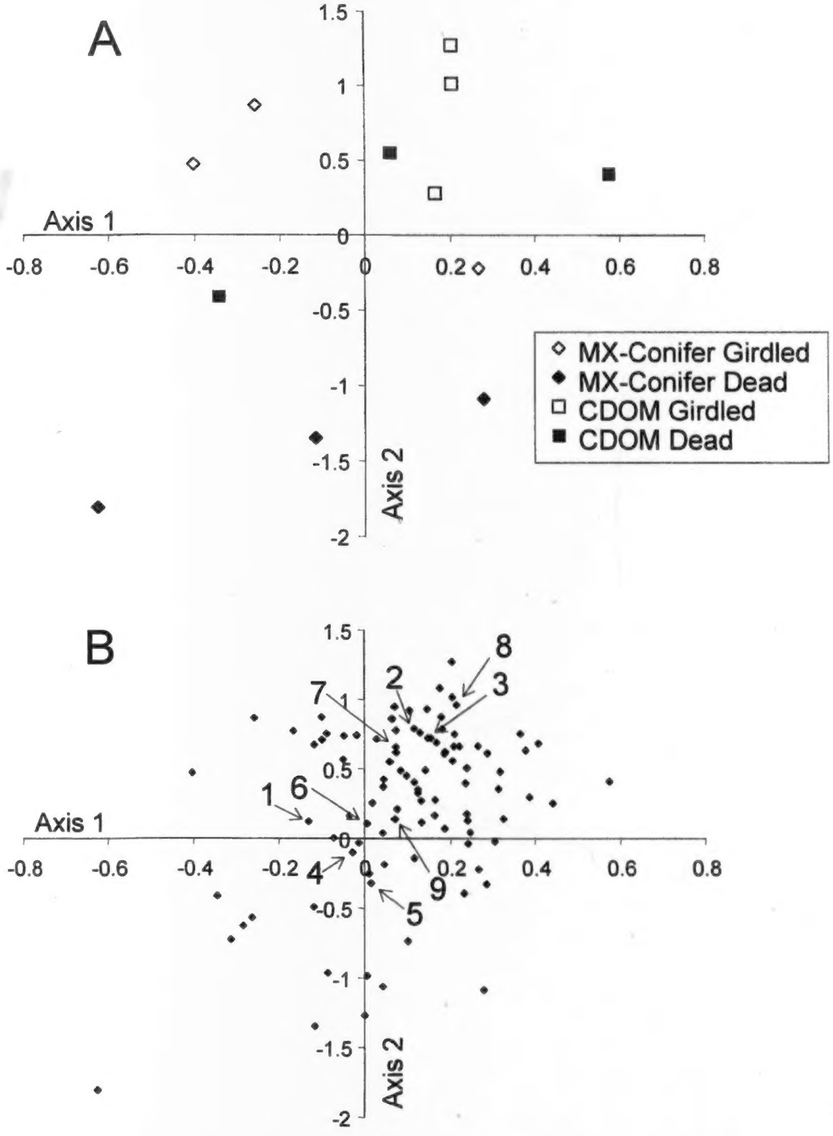

Figure 2-9 NMS ordination of 117 species and 12 samples from spruce snags in coniferous dominated or co-dominated cover types: A) samples in species space, and B) overlay of species on the initial ordination. Numbers correspond to Table 2-5, species with a significant indicator value to stand and mortality type.

Table 2-5 Significant indicator species indicators of spruce trees in coniferous dominated or co-dominated stands.

Ordination number	Family	Species	Total catch (beetles/day)	Cover type	Mortality factor	Observed indicator value	Indicator value from randomized tests	
							Mean± SD	P
1	Scolytidae	*Crypturgus borealis* Swaine	2.2518	CDOM	Girdled	79.6	46.1±12.27	0.02
2	Staphylinidae	*Phloeostiba lapponicus* (Zetterstedt)	0.2842	CDOM	Girdled	70.3	41.4±13.13	0.02
3	Rhizophagidae	*Rhizophagus brunneus* Horn	0.6633	CDOM	Girdled	61.5	40.3±9.03	0.02
4	Cerylonidae	*Cerylon castaneum* Say	0.0792	CDOM	Dead	80.8	37.4±16.68	0.022
5	Ciidae	*Dolichocis manitoba* Dury	0.1094	CDOM	Dead	79.1	37.2±16.22	0.022
6	Lathridiidae	*Corticaria serrata* (Paykull)	0.9170	CDOM	Dead	44.2	33.6±4.05	0.022
7	Colydiidae	*Lasconotus complex* LeConte	0.2899	CDOM	Girdled	50.8	36.9±8.2	0.035
8	Scolytidae	*Ips pini* (Say)	0.3987	CDOM	Girdled	93.2	46.6±20.46	0.037
9	Cryptophagidae	*Caenoscelis antennalis* (Casey)	0.5227	CDOM	Dead	50.8	37.3±6.66	0.045

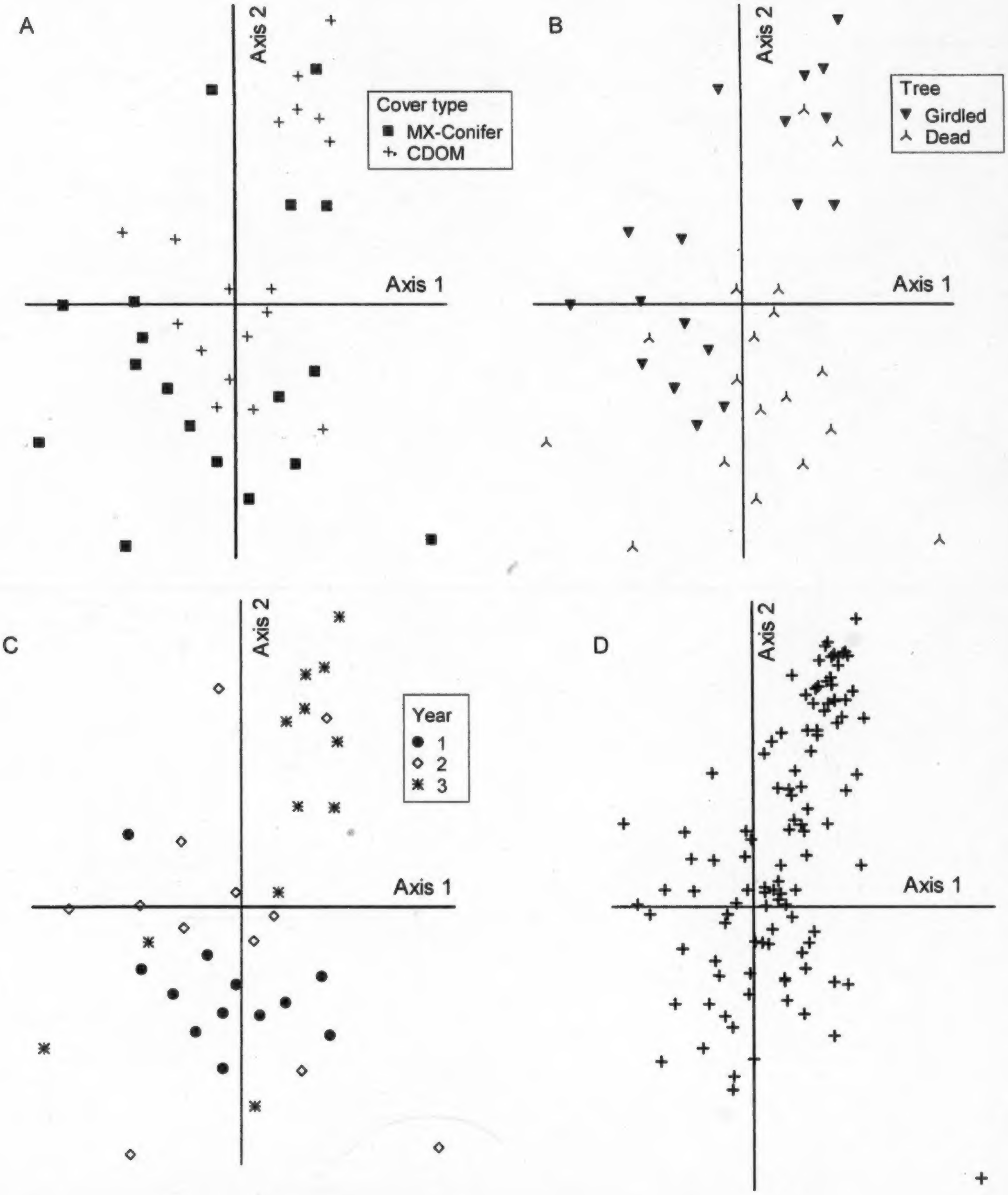

Figure 2-10 NMS ordination of 114 species and 36 samples from spruce snags in CDOM and MX-Spruce stands: A) samples coded by cover type; B) samples coded by tree mortality; C) samples coded by year, and D) species overlay.

Table 2-6 Significant indicator species of different years in CDOM and MX-Conifer stands trapped on girdled and naturally dead spruce trees.

Family	Species	Total catch (beetles/day)	Year	Mortality factor	Observed indicator value	Indicator value from randomized tests	
						Mean± SD	P
Rhizophagidae	*Rhizophagus dimidiatus* Mannerheim	0.7731	3	Girdled	87	32.4±12.11	0.003
Scolytidae	*Trypodendron lineatum* (Olivier)	5.0438	3	Girdled	99	54.5±15.53	0.003
Scolytidae	*Crypturgus borealis* Swaine	1.9647	3	Girdled	99	34.9±13.91	0.003
Staphylinidae	*Phloeostiba lapponicus* (Zetterstedt)	0.2687	3	Girdled	100	28.9±12.65	0.003
Colydiidae	*Lasconotus complex* LeConte	0.2511	3	Girdled	87	31.4±11.36	0.004
Scolytidae	*Dryocoetes affaber* (Mannerheim)	7.5064	3	Girdled	77	46.2±11.15	0.008
Scolytidae	*Scierus pubescens* Swaine	3.14	3	Girdled	79	48.7±10.87	0.01
Nitidulidae	*Epuraea linearis* Mäklin	2.5484	3	Girdled	90	61.8±13.82	0.013
Rhizophagidae	*Rhizophagus brunneus* Horn	0.0775	3	Girdled	76	37.7±12.59	0.014
Scolytidae	*Xylechinus montanus* Blackman	2.0771	3	Girdled	70	43.4±10.81	0.029
Ptiliidae	*Acrotrichis castanea* (Matthews)	0.0618	3	Dead	54	27.7±11.19	0.032
Scolytidae	*Scierus annectans* LeConte	0.1836	3	Dead	74	44.2±14.2	0.042
Melandryidae	*Xylita livida* (C.R.Sahlberg)	0.2903	1	Dead	63	37.6±12.54	0.05

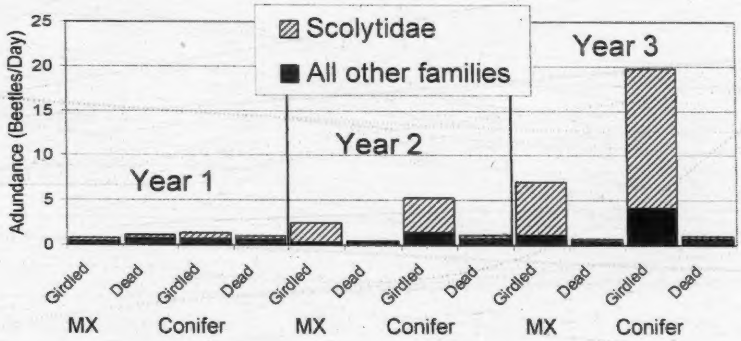

Figure 2-11 Catch of saproxylic beetles on girdled and naturally dead trees in conifer dominated and mixedwood cover types.

Multivariate Regression. Multivariate regression consistently produced a tree with 6 terminal nodes explaining 43% or the variation in the data (Fig. 2-12). The first split in the tree is based on the mean volume of white spruce in the stand. Stands with less than $0.25m^3$/ha had a similar beetle community. All the DDOM sites and two of the DDOMU sites are represented at node 1. Species indicator analysis on this node found 6 significant indicators (Table 2-7). The next split is based on tree mortality. All remaining traps on naturally dead trees are represented at node 2. This includes traps from DDOMU, MX, and CDOM. There was a single species (Table 2-7) found to be a significant indicator of this node. Stands with more than $3.152m^3$/ha of balsam poplar are represented in node 3. Traps represented in this node are from two CDOM stands. There are 21 significant indicators of this node (Table 2-7). The next split is between traps on deciduous trees and traps on white spruce trees. There are DDOMU and MX sites represented in terminal node 4. Species indicator analysis did not find any species to be significantly indicative of this node. The final split in the tree is based on the number of snags at intermediate stages of decay within 5m of the trap tree. Traps with any surrounding local snags resulted in the community at node 5. A single species was found to be a significant indicator of this node (Table 2-7). Traps without surrounding local snags around the trap tree resulted in node 6. Six species were designated as significant indicators of this node (Table 2-7).

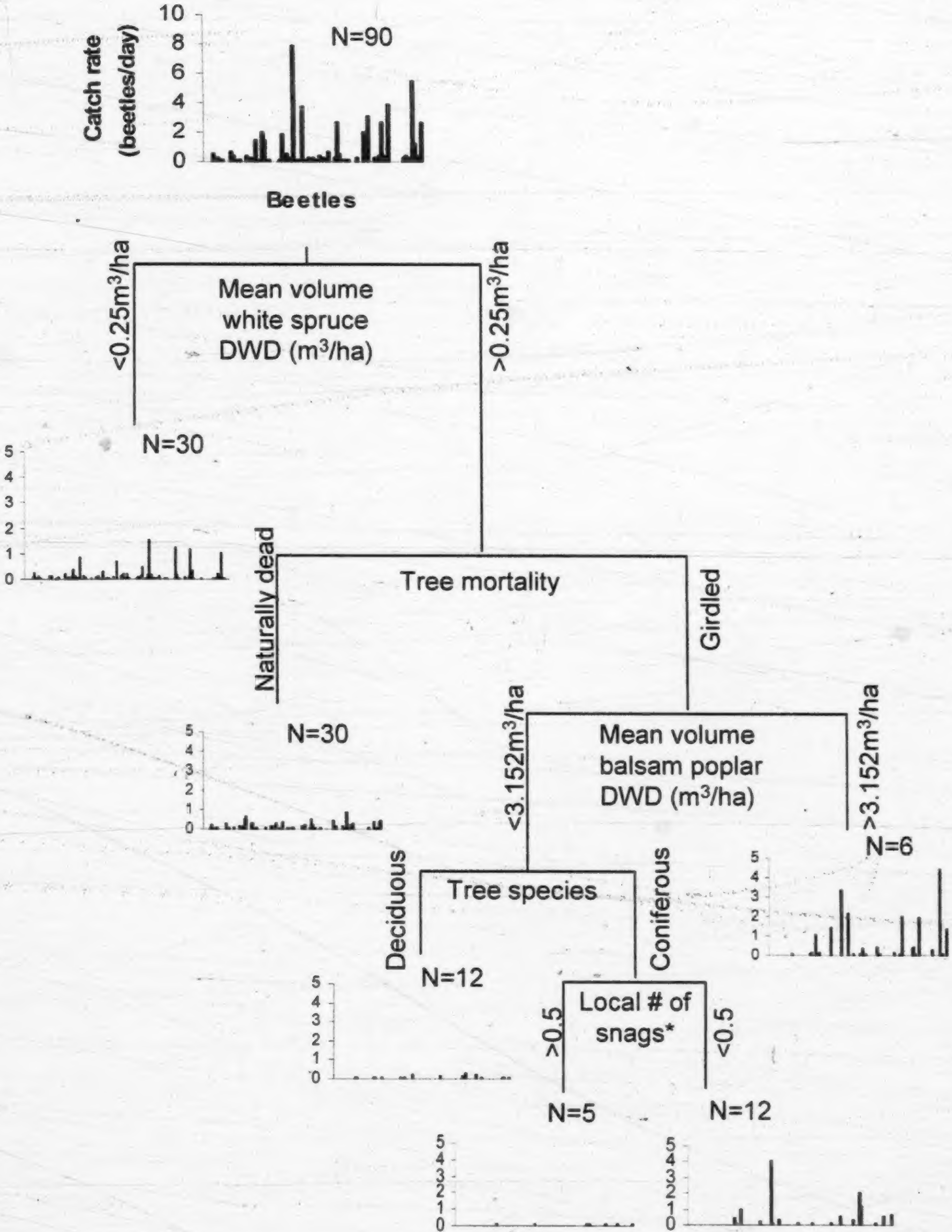
Catch rate (beetles/day)
10
8
6
4
2
0
N=90
Beetles
<0.25m³/ha
Mean volume white spruce DWD (m³/ha)
>0.25m³/ha
N=30
5
4
3
2
1
0
Naturally dead
Tree mortality
Girdled
N=30
<3.152m³/ha
Mean volume balsam poplar DWD (m³/ha)
>3.152m³/ha
N=6
Deciduous
Tree species
Coniferous
N=12
>0.5
Local # of snags*
<0.5
N=5
N=12

Figure 2-12 Multivariate regression tree of all sites. Graphs are abundance plots of all 189 saproxylic beetle species. Error 0.57, CV error 0.838, SE 0.0767.

Table 2-7 Significant indicator species of terminal nodes from multivariate regression tree in Figure 2-12.

Family	Species	Node	Observed indicator value	Indicator value from randomized tests	
				Mean± SD	P
Carabidae	*Platynus decentis* (Say)	1	41.4	20.7±5.12	0.001
Carabidae	*Calosoma frigidum* Kirby	1	41.1	11.9±6.21	0.005
Nitidulidae	*Glischrochilus siepmanni* W.J.Brown	1	43.2	13±7.18	0.007
Anobiidae	*Ptilinus lobatus* Casey	1	30	13.1±6.95	0.03
Elateridae	*Ampedus deletus* (LeConte)	1	27.4	13±6.29	0.03
Pyrochroidae	*Dendroides ephemeroides* (Mannerheim)	1	23.3	9.7±6	0.043
Ciidae	*Dolichocis manitoba* Dury	2	26.3	12.6±6.71	0.047
Scolytidae	*Dendroctonus rufipennis* (Kirby)	3	85.1	18.7±8.91	0.001
Staphylinidae	*Phloeonomus lapponicus* (Zetterstedt)	3	66.9	11.8±6.58	0.001
Cleridae	*Thanasimus undatulus undatulus* (Say)	3	65.7	12.2±6.47	0.001
Scolytidae	*Xylechinus montanus* Blackman	3	64.8	21.1±8.12	0.001
Scolytidae	*Scierus pubescens* Swaine	3	62.6	17.9±7.91	0.001
Scolytidae	*Polygraphus rufipennis* (Kirby)	3	60.8	20.2±8.26	0.001
Cryptophagidae	*Cryptophagus varus* Woodroffe & Coombs	3	55.3	11.9±7.14	0.001
Scolytidae	*Ips pini* (Say)	3	46.9	9.6±6.27	0.001
Cerambycidae	*Pogonocherus penicillatus* LeConte	3	45.6	9.6±5.84	0.001
Scolytidae	*Trypodendron lineatum* (Olivier)	3	73.3	22.7±10.49	0.002
Rhizophagidae	*Rhizophagus dimidiatus* Mannerheim	3	59.9	12.8±7.08	0.002
Nitidulidae	*Epuraea linearis* Mäklin	3	76.5	34.4±11.61	0.005
Corylophidae	*Molamba obesa* Casey	3	43.3	11.6±6.89	0.005
Scolytidae	*Crypturgus borealis* Swaine	3	47.3	14.3±8.04	0.006
Lathridiidae	*Melanophthalma villosa* (Zimmermann)	3	33.3	8.4±5.41	0.006

Family	Species	Node	Observed indicator value	Indicator value from randomized tests	
				Mean± SD	P
Cerambycidae	*Tetropium parvulum* Casey	3	42.4	24.7±5.18	0.007
Cerambycidae	*Phymatodes dimidiatus* (Kirby)	3	40.9	11.9±6.62	0.007
Scolytidae	*Dryocoetes autographus* (Ratzeburg)	3	31.8	8.6±5.05	0.008
Scolytidae	*Dryocoetes affaber* (Mannerheim)	3	38.2	13±7.18	0.014
Cryptophagidae	*Caenoscelis antennalis* (Casey)	3	48.1	22.5±8.68	0.017
Histeridae	*Hister* sp	3	30.9	17.3±5.91	0.028
Curculionidae	*Hylobius pinicola* (Couper)	3	25.8	10.4±7.03	0.041
Scolytidae	*Scierus annectans* LeConte	5	48.1	9.7±6.21	0.001
Colydiidae	*Lasconotus complex* LeConte	6	53.6	19±8.11	0.004
Curculionidae	*Pissodes rotundatus* LeConte	6	33.6	10.4±6.05	0.009
Clambidae	*Clambus pubescens* Redtenbacher	6	27.5	9.7±5.87	0.022

Discussion

This study begins to describe and clarify the determinants of saproxylic beetle assemblage structure in forest stands in the boreal forests of northern Alberta. Siitonen (2001) states that the main factors determining species composition in dead wood are tree species, stage of decay, co-occurring species of fungi (also involved in the decay), the quality and diameter of the trunk and the amount of surrounding CWD. The importance of most of these factors were underscored in the current study. The present work clearly demonstrates that tree species is a major factor determining saproxylic beetle assemblages. Faunal differences between girdled and dead trees were evident in every analysis, indicating that stage of decay also plays a major part in determining saproxylic beetle assemblages. Multivariate regression analysis demonstrates that CWD quantity and quality at multiple scales have a large influence on the saproxylic beetle assemblages. Furthermore, the relative abundance of live canopy tree species appears to play a role in determining composition of saproxylic beetle communities. As amplified below, this feature is especially relevant to conservation issues.

The influence of CWD quality. Trembling aspen and white spruce responded differently to girdling; spruce quickly succumbed to girdling, whereas most girdled aspen remained alive for the three years of the study, reflecting a large capacity for stem storage of carbohydrates in aspen. The capacity for girdled aspen to remain alive undoubtedly resulted in the low raw catch of saproxylic beetles collected from these trees. Rearing and subsequent debarking of bolts cut from these trees after completion of sampling demonstrated that no beetles inhabited girdled aspen trees even at the end of the study (Jacobs, unpublished data). Composition of beetle assemblages captured on aspen, as analyzed by NMS, differed markedly between girdled and dead trees, except for one stand in which one of the three girdled trees died, resulting in a beetle assemblage resembling that of naturally dead trees. Thus, girdled aspen trees are not similar to girdled spruce in terms of availability for colonization by saproxylic beetles. Although saproxylic beetles were trapped in low numbers on living girdled aspen, this cannot be taken as evidence of attraction to these trees as catches may be simply incidental (background noise) or beetles specifically attracted to the wound associated with girdling. Hammond et al. (2001) studied newly created trembling aspen CWM and found a lower abundance of beetles the first year of collection compared to the second year, suggesting that early colonizing species, primarily wood-borers, precondition the wood for a number of succeeding species.

Most white spruce appeared dead or were dying by the fall or spring after girdling, and none survived for more than a year. Multiple analyses revealed that there were significant differences between the beetle assemblages of recently girdled and dead spruce trees. Most of these differences can be attributed to the large increase in bark beetles (Scolytidae) and their natural enemies (Rhizophagidae, Cleridae, Colydiidae, Staphylinidae) over the three years of the study. The relative abundance of bark beetles increased every year of the study. The relatively low abundance of the initial year's collection reflected beetles attacking the tree, and the higher catches in the second and third years of collection reflected both beetles attacking the tree and those emerging. The increase in abundance of bark beetles also resulted in increased abundance of their predators.

Esseen et al. (1992, 1997) distinguished four main successional stages in saproxylic beetle assemblages in Fennoscandian forests, and these match well with successional stages observed in north-western Alberta. The first stage consisted primarily of bark beetles, and other phloeophagous beetles that require fresh phloem, and their predators; the fauna associated with girdled spruce trees represents this first stage of succession. Numerous phloem feeding beetles (*e.g.*, *Polygraphus rufipennis, Dryocoetes affaber, Trypodendron lineatum*) and their specific predators (*Rhizophagus brunneus*, *Lasconotus* complex, etc.) were significant indicators of recently dead and dying trees. The second successional stage was evident by the third year of sampling in girdled spruce when characteristic secondary phloem feeding beetles (*e.g.*, *Crypturgus borealis*) and fungivorous beetles (*e.g., Corticaria serrata*) started to arrive. The third stage of saproxylic beetle succession begins when the bark begins to fall off and polypores and their associated species arrive. However, no trees in this late stage of decay were examined in this study. Although Esseen et al. (1992, 1997) studied these characteristics of beetle succession in logs, I observed many similarities with snags, even though Siitonen (2001) points out that successional patterns in snags will differ significantly from those in logs. Because standing dead wood decays slower than logs, suitably detailed analysis of the decay process would likely recognize more distinct stages of snags.

It is well known that many saproxylic beetles express a narrow range in host tree preferences (Arnett and Thomas 2001a, b). Such preferences for aspen or spruce trees could be explicitly studied in the mixedwood stands as, in this cover type, trees and snags of each species were present in a common stand environment. In fact, the general structure of the beetle community differed conspicuously between the two potential host species. Traps on aspen trees in the mixedwood stand, like traps placed on aspen trees elsewhere, collected a wide diversity of species but fewer individuals than were collected on coniferous trees. Without tree death, girdled aspens are apparently unattractive to many potential attackers, both insects and fungi. Furthermore, ordinations of saproxylic beetle assemblages revealed distinct clusters on both spruce and aspen trees. Beetle assemblages from girdled spruce trees were the most dissimilar to other assemblages, partly reflecting the large number of beetles collected from these trees. Approximately half (65) of the 129 species collected in the mixedwood stand were collected from a single tree species, and a number of beetle species (*e.g.*, *Dryocoetes affaber, Crypturgus borealis, Lasconotus* complex) seem to be most closely associated with girdled spruce trees.

The influence of CWD quantity. Distribution of CWD across the EMEND landscape is consistent with typical CWD successional models (Sprugel 1984, Agee and Huff 1986, Spies et al. 1988, Duvall and Grigal 1999). Little CWD from the initial disturbance is seen in aspen stands at the EMEND site as these were already mature aspen stands which had existed at least 80 years since the last major disturbance. Multivariate regression analysis illustrates that importance of CWD to saproxylic beetle assemblages. Five stands (30 traps) all without white spruce DWD separate out at the first node. CWD comes out again in the analysis dividing stands based on the volume of balsam poplar DWD and again on the number of local snags.

Studies from Fennoscandia demonstrate that CWD in managed forests has dropped 90-98% from the primeval condition (Siitonen 2001). Furthermore, Siitonen et al. (2000) was able to show that volumes of CWD were tenfold greater in natural forests than managed forests and that numbers of large-diameter coniferous and deciduous trees were 25 and 35 fold different.

The influence of stand successional stage and cover type. Composition of saproxylic beetle assemblages in both aspen and spruce were influenced by the stand cover type (*i.e.*, the relative proportional abundance of aspen and spruce in the overstory), which is representative of different stages of stand succession. Ordination demonstrated a strong influence of cover type on the composition of spruce-associated beetle assemblages as CDOM and MX stands formed distinct clusters in ordination space. When the species overlay is compared to the sample ordination, it is clear that a large number of species occur only in or are mostly associated with CDOM stands. Species indicator analysis revealed that 9 species were significant indicators, all of naturally dead and girdled trees in the CDOM stand, and that none were indicative of spruce in MX stands. The most abundant indicator species is a secondary phloeophagous bark beetle, *Crypturgus borealis*, which must utilize existing entrance holes made by other scolytids to gain access to the phloem for reproduction. Other indicators include the bark beetle, *Ips pini*, three bark beetle predators and four fungivorous species. It is possible that these conifer specialists are colonizing from surrounding spruce CWD. Although CWD differed little between CDOM and MX stands, a greater proportion of the CWD in MX-spruce stands is from the dying deciduous cohort than from CDOM stands. Thus, it is likely that the greater amount of spruce CWD could increase the ability of conifer specialist beetles to colonize suitable habitats in CDOM stands.

There was no evidence of influence of stand type on aspen-associated assemblages when catch data were analyzed; however, analysis based on species presence or absence showed differences in assemblage structure among DDOM, DDOMU and MX stands. DDOMU stands had a beetle composition intermediate between the DDOM stands and the MX-aspen stands. Interestingly, one of the significant indicators of the MX-aspen stands, *Trypodendron lineatum*, is a spruce specialist that was so abundant that the beetles caught on aspen trees must simply represent those trying to disperse within the stands. Species indicator analysis showed that 12 species were significant indicators of the DDOM and this group included both wood boring beetles (*e.g.*, *Ptilinus lobatus*) and fungivores (*e.g.*, *Melophthalma villosa* and *Melandrya striata*). The distinctness of saproxylic assemblages in the DDOM stands suggest that these stands may have unique habitat features and are important for the conservation of saproxylic beetles. It is possible that the unique habitat characteristics may be related to the presence of legacy CWD, *i.e.*, CWD originating from the previous stand. Legacy CWD, which is often of larger diameter than the CWD originating from the current stand, is expected to be more abundant in DDOM stands and declines in abundance, due to decay, in later successional stages.

Implications for Forest Management.

Deciduous dominated boreal stands are generally poorly studied in other parts of the world due to a lack of stands remaining after centuries of intensive management and stand conversion. Studies emerging from North America (Hammond 1997, Hammond et al. 2001, Hammond et al. 2004) show that these stands have a unique and diverse saproxylic community. The lack of these types of stands in the boreal forests of other parts of the world due to intensive forestry should increase the importance of these stands for conservation efforts. The importance of deciduous trees in conservation of saproxylics has been recognized in northern Europe (Martikainen 2001).

It is clear that both CWD quality and quantity, and the relative abundance of canopy trees have strong effects on saproxylic beetle assemblages. Given what we presently understand about saproxylic beetles in the boreal zone of North America, conservation of these important faunal elements will require retention of the full range of cover types on the forest landscape. There is a need to identify the specific qualities and quantities of CWD Esseential to maintaining diverse saproxylic beetle communities. Present understanding (*e.g.*, Siitonen 2001) suggests that this will not be a short list. Our present data suggest that all boreal stand types are associated with somewhat distinct saproxylic communities that likely originate in the subtleties of CWD succession in different mixes of tree species. In order to conserve this ecologically important group of insects and its functions in nutrient cycling, we must retain appropriately scaled mixes of all natural relative densities of CWM characteristic of the major cover types on forested landscapes.

Literature Cited

Agee, J. K., and M. H. Huff. 1986. Fuel succession in a western hemlock/Douglas fir forest. Canadian Journal of Forest Research **17**:697-704.

Arnett, R. H. J., and M. C. Thomas. 2001a. American beetles v. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, Florida.

Arnett, R. H. J., and M. C. Thomas. 2001b. American beetles v. 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, Florida.

Bousquet, Y. 1991. Checklist of beetles of Canada and Alaska. Agriculture Canada, Ottawa, Ont.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. G. Stone. 1984. Classification and regression trees. Wadsworth International Group, Belmont, California, USA.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics **43**:783-791.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Colwell, R. K. 2000. EstimateS Statistical Estimation of Species Richness [online]. Available from http://viceroy.eeb.uconn.edu/EstimateS. php [updated 16 September 2002; cited 18 May 2004].

De'Ath, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. **83**:1105-1117.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Duvall, M. D., and D. F. Grigal. 1999. Effects of timber harvesting on coarse woody debris on red pine forests across the Great Lake states, U.S.A. Canadian Journal of Forest Research **29**:1926-1934.

Ehnström, B. 2001. Leaving dead wood for insects in boreal forests - suggestions for the future. Scandinavian Journal of Forest Research **16**:91-98.

Esseen, P. A., B. Ehnström, L. Ericson, and K. Sjöberg. 1992. Boreal forests the focal habitats of Fennoscandia. Elsevier Applied Science, London.

Esseen, P. A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal Forests. Ecological Bulletin **46**:16-47.

Hammond, H. E., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research **31**:1175-1183.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. Canadian Entomologist **129**:1009-1033.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research **34**:1-19.

Hatch, M. H. 1953a. The beetles of the Pacific Northwest. pt1. Introduction and Adephaga. University of Washington Press, Seattle.

Hatch, M. H. 1953b. The beetles of the Pacific Northwest. pt2. Staphyliniformia. University of Washington Press, Seattle.

Hatch, M. H. 1953c. The beetles of the Pacific Northwest. pt3. Pselaphidae and Diversicornia. University of Washington Press, Seattle.

Hatch, M. H. 1953d. The beetles of the Pacific Northwest. pt4. Macrodactyles. University of Washington Press, Seattle.

Hatch, M. H. 1953e. The beetles of the Pacific Northwest. pt5. Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia. University of Washington Press, Seattle.

Käila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica **29**:21-23.

Magurran, A. E. 1988. Ecological diversity and its measurment. Princeton University Press, Princeton, New Jersey.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletin **49**:205-218.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation **94**:199-209.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, OR.

McCune, B., and M. J. Medford. 1999. PCOrd software: multivariate analysis of ecological data. MJM Software. Gleneden Beach, OR.

McGill, W. E., and J. R. Spence. 1985. Soil fauna and soil structure: feedback between size and architecture. Quaestiones Entomologicae **21**:645-654.

R. Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.

Reichle, D. E. 1977. The role of soil invertebrates in nutrient cycling. Ecological Bulletins **25**:145-156.

Rowe, J. S. 1994. A New Paradigm for Forestry. **70**:565-568.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins **49**:11-41.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russion Karelia. Scandinavian Journal of Forest Research **9**:185-191.

Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management **128**:211-225.

Simila, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation **106**:19-27.

Sippola, A. L., J. Siitonen, and P. Punttila. 2002. Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. Annales Zoologici Fennici **39**:69-86.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe Publications, Strasbourg.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in douglas-fir forests of western Oregon and Washington. Ecology **69**:1689-1702.

Sprugel, D. 1984. Changes in biomass components through stand development in wave-generated balsam fir forests. Canadian Journal of Forest Research **15**:269-278.

SPSS. 2001. SPSS for windows. SPSS Inc., Chicago, Illinois.

Van Wagner, C. E. 1968. The line intersect method for forest fuel sampling. Forest Science **14**:20-26.

White, R. E. 1983. A Field Guide to the Beetles: of North America. Houghton Mifflin, Boston.

Work, T. T., D. P. Shorthouse, J. R. Spence, W. J. A. Volney, and D. W. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research **34**:417-430.

Appendix 2-A

Saproxylic beetles collected from flight intercept traps on dead and girdled trees from deciduous dominated (DDOM), deciduous dominated with a developing coniferous understory (DDOMU), Mixedwood (MX), and coniferous dominated (CDOM) stands

Family	Species	Years collected	Forest cover types	Tree type
Anobiidae	*Ernobius* sp.	1999, 2001	MX, CDOM	Girdled
	Xestobium sp.	1999	CDOM	Dead
	Dorcatoma moderata R.E.White	1999-2000	DDOM, MX	Girdled, Dead
	Hemicoelus carinatus (Say)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Microbregma emarginatum (Duftschmid)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Ptilinus lobatus Casey	1999	MX	Girdled
	Tricorynus densus (Fall)	1999	DDOM, DDOMU	Dead
	Utobium elegans (Horn)	1999-2001	DDOM, DDOMU, CDOM	Girdled, Dead
Cantharidae	*Dichelotarsus piniphilus* (Eschscholtz)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Carabidae	*Agonum retractum* LeConte	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Agonum sordens Kirby	2000-2001	DDOM, DDOMU	Dead
	Bembidion mutatum Gemminger & Harold	2000	DDOM	Dead
	Calathus advena (LeConte)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Calathus ingratus Dejean	1999-2001	DDOM, MX	Girdled, Dead
	Calosoma frigidum Kirby	1999-2001	DDOM, DDOMU	Girdled, Dead
	Platynus decentis (Say)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Pterostichus adstrictus Eschscholtz	1999, 2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead

Family	Species	Years collected	Forest cover types	Tree type
	Stereocerus haematopus (Dejean)	1999-2000	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Cephaloidae	*Cephaloon tenuicorne* LeConte	1999-2000	DDOM, MX	Dead
Cerambycidae	*Acmaeops proteus proteus* (Kirby)	1999	CDOM	Girdled
	Grammoptera subargentata (Kirby)	1999-2000	DDOM, DDOMU, MX	Girdled, Dead
	Phymatodes dimidiatus (Kirby)	2000-2001	CDOM	Girdled
	Pogonocherus penicillatus LeConte	2000-2001	CDOM	Girdled
	Spondylis upiformis Mannerheim	1999	DDOM	Girdled
	Tetropium parvulum Casey	1999-2001	CDOM	Girdled, Dead
	Trachysida aspera aspera (LeConte)	1999-2001	DDOM, DDOMU	Dead
	Trachysida mutabilis (Newman)	1999	DDOM, DDOMU	Girdled, Dead
Cerylonidae	*Cerylon castaneum* Say	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Ciidae	*Cis fuscipes* Mellié	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Cis biarmatus Mannerheim	1999	DDOM	Dead
	Dolichocis manitoba Dury	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Octotemnus laevis Casey	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
	Orthocis punctatus (Mellié)	1999	DDOM	Girdled
	Sulcacis curtula (Casey)	1999	DDOM	Dead
Clambidae	*Clambus pubescens* Redtenbacher	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Cleridae	*Thanasimus undatulus undatulus* (Say)	1999-2001	DDOMU, CDOM	Girdled
Colydiidae	*Lasconotus complex* LeConte	2000-2001	CDOM	Girdled

Family	Species	Years collected	Forest cover types	Tree type
Corylophidae	*Molamba obesa* Casey	1999-2001	DDOM, CDOM	Girdled, Dead
Cryptophagidae	*Atomaria* sp.	1999-2001	DDOMU, MX, CDOM	Dead
	Caenoscelis antennalis (Casey)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Cryptophagus tuberculosus Maklin	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Cryptophagus varus Woodroffe & Coombs	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
	Ephistemus globulus (Paykull)(+)	2001	CDOM	Girdled, Dead
	Henoticus serratus (Gyllenhal)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Henotiderus obesulus (Casey)	1999-2001	DDOM, DDOMU, MX	Girdled, Dead
	Salebius octodentatus (Maklin)	1999, 2001	DDOM, MX	Dead
Cucujidae	*Cucujus clavipes puniceus* Mannerheim	1999-2001	DDOM, DDOMU, MX	Girdled, Dead
	Dendrophagus cygnaei Mannerheim	1999	DDOM, DDOMU	Girdled, Dead
	Pediacus fuscus Erichson	1999	DDOM, DDOMU, CDOM	Girdled, Dead
Curculionidae	*Cossonus pacificus* Van Dyke	1999-2001	DDOM, DDOMU, CDOM	Girdled, Dead
	Cossonus quadricollis Van Dyke	1999-2000	DDOM	Girdled, Dead
	Hylobius pinicola (Couper)	2000-2001	CDOM	Girdled
	Magdalis subtincta LeConte	1999-2000	DDOM, DDOMU, MX	Girdled, Dead
	Pissodes rotundatus LeConte	1999-2001	MX, CDOM	Girdled
	Rhyncolus brunneus Mannerheim	2001	MX	Dead
Dermestidae	*Dermestes lardarius* Linné	2000-2001	DDOM	Dead
Elateridae	*Ampedus deletus* (LeConte)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead

Family	Species	Years collected	Forest cover types	Tree type
	Ampedus miniipennis (LeConte)	1999-2000	DDOM, CDOM	Girdled
	Ctenicera resplendens (Eschs.)	1999-2001	DDOM, DDOMU, CDOM	Girdled, Dead
	Denticollis denticornis (Kirby)	1999-2000	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Erotylidae	*Triplax antica* LeConte	2000	DDOM	Dead
	Triplax californica LeConte	1999-2001	DDOM, DDOMU, MX	Girdled, Dead
	Triplax thoracica Say	1999, 2001	DDOM, DDOMU	Dead
Eucinetidae	*Eucinetus punctulatus* LeConte	1999, 2001	DDOM, CDOM	Girdled, Dead
Eucnemidae	*Epiphanis cornutus* Eschscholtz	2000-2001	DDOMU, MX, CDOM	Dead
Histeridae	*Saprinus* sp	2000	DDOM	Dead
	Hister sp	2000-2001	MX, CDOM	Girdled, Dead
Hydrophilidae	*Cercyon herceus frigidus* Smetana	1999	MX	Girdled
Lampyridae	*Ellychnia corrusca* (Linné)	2001	DDOM	Girdled
Lathridiidae	*Cartodere constricta* (Gyllenhal)	1999, 2001	DDOM, DDOMU	Dead
	Corticaria serrata (Paykull)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Corticaria sp.	2001	DDOMU, CDOM	Girdled
	Enicmus mimus Fall	1999	DDOMU, MX, CDOM	Girdled, Dead
	Enicmus tenuicornis LeConte	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Lathridius hirtus Gyllenhal	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Lathridius minutus (Linné)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Melanophthalma villosa (Zimmermann)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead

Family	Species	Years collected	Forest cover types	Tree type
	Stephostethus liratus (LeConte)	1999	DDOM	Girdled, Dead
Leiodidae	*Agathidium* sp.A	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Agathidium sp.B	1999	DDOM, DDOMU	Dead
	Anisotoma sp.	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Lycidae	*Dictyopterus thoracicus* (Randall)	1999	DDOMU	Girdled
Lymexylidae	*Hylecoetus lugubris* Say(+)	1999	DDOM	Dead
Melandryidae	*Dircaea liturata* (LeConte)	1999-2000	DDOM, DDOMU	Dead
	Enchodes sericea (Haldeman)	1999-2000	DDOMU, CDOM	Girdled, Dead
	Melandrya striata Say	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Orchesia castanea (Melsheimer)	1999, 2001	DDOM, DDOMU, MX	Girdled, Dead
	Serropalpus substriatus Haldeman	1999-2001	DDOM, DDOMU, MX	Dead
	Xylita laevigata (Hellenius)	2000	DDOM	Dead
	Xylita livida (C.R.Sahlberg)	1999-2001	MX, CDOM	Girdled, Dead
	Zilora hispida LeConte	1999	CDOM	Dead
Mycetophagidae	*Mycetophagus quadriguttatus* P.W.J.Muller	1999, 2001	DDOM, DDOMU, CDOM	Girdled, Dead
	Mycetophagus distinctus Hatch	1999-2000	DDOM, DDOMU, MX, CDOM	Girdled, Dead
Nitidulidae	*Epuraea linearis* Mäklin	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Glischrochilus moratus W.J.Brown	1999-2001	DDOM, DDOMU, MX	Girdled, Dead
	Glischrochilus sanguinolentus (Olivier)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Glischrochilus siepmanni W.J.Brown	1999-2001	DDOM, DDOMU, MX	Girdled, Dead

Family	Species	Years collected	Forest cover types	Tree type
	Glischrochilus vittatus (Say)	2000	DDOM	Dead
Pselaphidae	*Batrisodes* sp.	2001	DDOM	Girdled, Dead
Ptiliidae	*Acrotrichis castanea* (Matthews)	1999-2001	DDOM, DDOMU, CDOM	Girdled, Dead
Pyrochroidae	*Dendroides ephemeroides* (Mannerheim)	1999, 2001	DDOM, DDOMU	Girdled, Dead
	Schizotus cervicalis Newman	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
Pythidae	*Pytho* sp.	2000	DDOM	Dead
Rhizophagidae	*Rhizophagus brunneus* Horn	2000-2001	MX, CDOM	Girdled, Dead
	Rhizophagus dimidiatus Mannerheim	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Rhizophagus remotus LeConte	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
Scolytidae	*Carphoborus andersoni* Swaine	2000	CDOM	Girdled
	Cryphalus ruficollis Hopkins	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
	Crypturgus borealis Swaine	1999, 2001	DDOM, DDOMU, CDOM	Girdled, Dead
	Dendroctonus rufipennis (Kirby)	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
	Dryocoetes affaber (Mannerheim)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Dryocoetes autographus (Ratzeburg)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Ips pini (Say)	2001	CDOM	Girdled
	Phloeotribus lecontei Schedl	2001	MX, CDOM	Dead
	Pityogenes plagiatus plagiatus (LeConte)	2001	CDOM	Girdled, Dead
	Pityophthorus sp.	1999	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Polygraphus rufipennis (Kirby)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead

Family	Species	Years collected	Forest cover types	Tree type
	Scierus annectans LeConte	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
	Scierus pubescens Swaine	1999-2001	MX, CDOM	Girdled, Dead
	Scolytus piceae (Swaine)	2000	CDOM	Dead
	Trypodendron lineatum (Olivier)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Trypodendron retusum (LeConte)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Trypodendron rufitarsis (Kirby)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Xylechinus montanus Blackman	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
Scydmaenidae	*Euconnus semiruber* Casey	2001	MX	Girdled
Sphindidae	*Odontosphindus clavicornis* Casey	1999-2001	DDOM, DDOMU, MX	Girdled, Dead
Staphylinidae	*Acidota crenata* (Fabricius)	1999-2001	DDOM, MX, CDOM	Girdled, Dead
	Acidota quadrata (Zetterstedt)	1999	DDOMU	Girdled
	Anotylus sobrinus (LeConte)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Bisinius tereus Smetana	1999-2001	DDOM, MX, CDOM	Girdled, Dead
	Bolitobius horni Campbell	1999	MX	Dead
	Carphacis nepigonensis (Bernhauer)	1999	DDOM	Dead
	Gabrius brevipennis (Horn)	1999, 2001	DDOMU, CDOM	Dead
	Ischnosoma splendidum (Gravenhorst)	2000-2001	MX	Girdled, Dead
	Lathrobium fauveli Duvivier	1999-2000	DDOM, DDOMU, MX	Girdled, Dead
	Lordithon bimaculatus (Couper)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Lordithon fungicola Campbell	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead

Family	Species	Years collected	Forest cover types	Tree type
	Lordithon longiceps (LeConte)	1999-2001	DDOM, MX, CDOM	Dead
	Megarthrus sinuaticollis Boisduval & Lacordaire	2000-2001	CDOM	Girdled
	Mycetoporus americanus Erichson	2000-2001	DDOM, DDOMU	Girdled, Dead
	Nudobius cephalus (Say)	1999-2001	DDOM	Girdled, Dead
	Olisthaerus sp.	1999-2001	DDOM, MX, CDOM	Girdled, Dead
	Omalium foraminosum Maklin	2001	MX, CDOM	Girdled, Dead
	Philonthus cyanipennis (Fabricius)	1999, 2001	DDOM, MX	Girdled
	Phloeostiba lapponicus (Zetterstedt)	2001	MX, CDOM	Girdled, Dead
	Quedius criddlei (Casey)	1999	MX	Dead
	Quedius fulvicollis (Stephens)	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Quedius plagiatus Mannerheim	1999-2001	DDOMU, MX, CDOM	Girdled, Dead
	Quedius rusticus Smetana	2000	MX, CDOM	Dead
	Quedius simulator Smetana	1999	DDOM, DDOMU, MX	Dead
	Quedius transparens Motschulsky	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Quedius velox Smetana	1999-2001	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Siagonium punctatum LeConte	1999, 2001	CDOM	Girdled
	Staphylinus pleuralis LeConte	2001	MX	Dead
	Stenus austini Casey	2000	DDOM	Dead
	Tachinus frigidus Erichson	1999, 2001	CDOM	Girdled, Dead
	Tachinus quebecensis Robert	1999	DDOMU	Girdled

Family	Species	Years collected	Forest cover types	Tree type
Trogositidae	*Ostoma ferruginea* (Linné)	1999-2000	DDOM, DDOMU, MX, CDOM	Girdled, Dead
	Thymalus marginicollis Chevrolat	1999-2001	DDOM, DDOMU, CDOM	Girdled, Dead

Chapter 3 Attraction of epigaeic and saproxylic beetles to a burned stand

Introduction

Forest management in Canada has recently moved towards an ecosystem management approach that attempts to emulate the effects of natural disturbance, such as wildfire, in forest harvest and regeneration (Haeussler and Kneeshaw 2003). It is hypothesized that by harvesting trees to produce landscape-level patterns similar to those produced by wildfire, ecosystem processes and functions will be maintained (Hunter 1993). However, in order to emulate natural patterns we must better understand how species and ecosystem processes respond to natural disturbances.

Wildfire is a major driver of disturbance regimes in North American boreal forests (Johnson 1992, Payette 1992). In the last 150 years there has been a decrease in fire frequency, with a punctuated change in 1945 (Johnson et al. 1999), about the time of initiation of concerted fire suppression programs. Fire suppression has resulted in forests with over 3 times the normal fuel loads (Clark 1990), which contributes to larger, more severe fires. With improved fire suppression reducing the frequency of fires and increased forest harvest, harvesting has become the largest disturbance on many boreal North American landscapes.

Burned forests support a unique insect fauna. Although many species that occur in burned forests are generally favoured by disturbance and also occur in other open habitat forests (Lundberg, 1984; Holliday, 1991; Ahnlund & Lindhe 1992; Kaila et al. 1997), there are numerous insects that are restricted to burned habitats for one or a few generations just after fire (Evans, 1971; Wikars, 1992; Jajoz 2000). Insects are thought to be attracted to burns because they are adapted to the warmer microclimate or reduced competition (Holliday 1991), the substrates created by fire are necessary for some part of the insect's life-cycle (Danks and Foottit 1989), or they feed on fire-adapted fungi growing in burned wood (Muona and Rutanen 1994). Little is known about the exact role of these 'pyrophilous' species, but it is thought that they might be involved in forest succession or alter the unique habitat created by fire to allow successful recovery of the forest (Hammond et al. 2001, Siitonen 2001). As a result, conservation of these insects could be important to maintaining natural processes in disturbed forests. At the very least these species are a unique component of forest biodiversity.

Beetles, in particular, have been the focus of numerous studies of the effects of wildfire. Work on epigaeic, ground dwelling beetles (Richardson and Holliday 1982, Holliday 1984, 1991, 1992, Wikars 1992, 1995, 1997, Wikars and Schimmel 2001, Wikars 2002) has shown that many species are closely associated with fire, and that there is a distinct change in the beetle assemblage following fire. Additionally, Gandhi et al. (2001) found that sub-alpine forest patches left following fire were typically older than the surrounding forest, indicating they have been skipped by fire events multiple times in succession. The unique properties of these unburned 'fire skips' supported an assemblage of epigaeic beetles different from the surrounding burned forest and undisturbed forest. Speight (1989) called specific attention to 'saproxylic' insects as those that depend, during some part of the life cycle, upon dead wood, wood-inhabiting fungi or the presence of other saproxylic organisms. Studies of saproxylic beetles (Wikars 1992, Muona and Rutanen 1994, Wikars 1997) have also identified numerous species, including bark beetles (Scolytidae), predators, and species associated with fungi, that are attracted to recently burned forests.

It is important to understand how beetles respond to fire, and especially how they react to the mosaic of habitats created from fire, if we are going to fully emulate the spatial patterns created by fire and its ecological roles. In this study, I monitored the distribution of epigaeic and saproxylic beetles within a burned white spruce, *Picea glauca* (Moench) Voss, dominated forest to examine the within-stand dynamics of these two functional groups of beetles. Specifically, my objectives were to: 1) to determine which beetle species are attracted to burned stands in northern Alberta; 2) to determine if species presence and abundance are correlated with fire intensity, and 3) to document changes (succession) in the beetle communities in years following fire. Given that some species have a close association with fire, I expected assemblages of beetles to differ between the burned areas and the unburned skips. Furthermore, I expected that local fire intensity would have a positive affect on the abundance of pyrophilous species.

Materials and Methods

Study Sites. The field aspects of this study were conducted at the Ecosystem Management by Emulating Natural Disturbance (EMEND) research site. EMEND is located in the Clear Hills Upland, Lower Foothills ecoregion of northern Alberta, approximately 90km north-west of Peace River (56° 46' 13"N, 118° 22' 28"W). The elevation on the site ranges from 677m to 880m. The soils at the site are fine-textured lacustrian (Work et al. 2004).

The study site used was a single 10ha stand, *c.* 100 years old, that was burned in July of 1999. The dominant canopy tree was white spruce with a small proportion of black spruce (*Picea mariana* (Miller)) and lodgepole pine (*Pinus contorta* Dougl.). Detailed surveys following the fire revealed 3 reasonably distinct burn intensity classes, hereafter referred to as treatments: 1) "skips", areas that had no evidence of fire, 2) "light burns", areas where patches of the duff layer had burned and most of the trees were still standing and 3) "severe burns", areas where most of the duff layer had burned and most of the trees had fallen. Four sites of each treatment, each *c.*100-200 m^2 in area, were established at least 50m apart and isolated from areas of similar treatment by at least 100m.

Only a single burned spruce stand was available for study at the EMEND experimental site at the time this fieldwork was conducted. Thus, replication in this study ensures only that general statements about the beetle assemblages in each treatment are robust. Replication of sites within this stand does not strongly support inferences about burned stands in general. However, such studies have merit in clearly defining patterns observed among treatments, given the most homogeneous set of background conditions possible for a field study. Over time, compilation of a series of such studies may lead to stronger inferences about general patterns among stands.

Sampling Methods and Identification. Epigaeic beetles were sampled using pitfall traps, consisting of an outer permanent (1L) cup and a removable (500ml) inner cup (Spence and Niemelä 1994). Traps were filled with 2-3cm of ethylene glycol as a killing agent and preservative and covered with an elevated 10cm x 10cm wood roof. Traps were emptied every 2-3 weeks throughout the frost free periods (May-August) in two consecutive years following the fire (2000 & 2001). Two pitfall traps located at least 10m apart were placed in each of the 4 sites of each treatment, for a total of 24 traps. In skips both traps were placed in the duff with the top of the cups flush with the litter layer. In light burns, one trap (Trap A) was placed in the duff layer, and the other trap was placed in an adjacent patch where the duff layer had been burned, flush with the top of the remaining mineral soil. In severe burns, both traps were placed in the mineral soil where the entire duff layer had been burned. In skips and severe burns, traps were arbitrarily labeled A and B.

Saproxylic beetles were sampled with passive barrier (window) traps, similar to those deployed by Hammond (1997), as modified from Käila (1993). Traps consisted of a clear piece of plastic (Plexiglass®), 1.5mm x 20cm x 30cm attached perpendicularly to trees to intercept insects on or near the tree. Insects then passed through a cloth funnel attached to the bottom of the interception panel, and were collected in a small plastic bag filled with ethylene glycol at the bottom of the funnel. This plastic bag was replaced with a new bag of fresh ethylene glycol every 2-3 weeks throughout the sampling period.

Passive barrier traps were chosen as they are an unbiased sampling method for flying arthropods orienting to dead wood, are easy to replicate in quantity, and provide large data sets suitable for community level statistical analysis. Traps were placed in all 4 sites of each treatment. At all sites, one trap was placed on a snag that had died naturally before the fire. Snags were chosen that were estimated to have died in the last 2-5 years, based on physical characteristics (all foliage dropped, but most bark and small branches retained) and were at least 8cm in diameter at breast height (DBH). Snags were chosen that were a similar diameter to the rest of the trees in the stand. At each site a second trap was placed on a tree killed by girdling. Trees were girdled using a hatchet to cut a band at least 7cm wide to the depth of the sapwood at a height of approximately 50cm. Trees chosen for girdling were located 10m to 30m from the snag and representative of the average diameter of trees in the stand. A third trap was placed on a fire-killed snag at each site in the light burn and severe burn treatments. In total 32 traps were deployed. The 'windows' of traps were located at approximately 1.5 m above ground on snags. Snags selected in the skips showed no evidence of fire damage, whereas snags selected in the light burns had some evidence of burning at the base, and those selected in the severe burns areas had obvious scorching, generally to a height of at least 5m.

All beetles were identified in the laboratory to the lowest taxonomic level possible based on current literature and local expertise. In most cases, species-level identification was possible except for the Aleocharinae (Staphylinidae), and some genera in the Nitidulidae, Lathridiidae and Leiodidae. Beetles were classified as epigaeic if they are commonly found or known to live on the forest floor and as saproxylic based on the definition by Speight (1989). Family and generic nomenclature follows that of Arnett (2001a, 2001b) and species nomenclature follows that of Bousquet (1991). Synoptic collections of all beetles were deposited in the insect museums at the University of Alberta and the Northern Forestry Centre, Canadian Forest Service.

Data Analysis. The beetle catch in each trap was standardized to number of individuals per day to adjust for uneven sampling effort resulting from animal-caused disturbance of some traps. All saproxylic species from the passive barrier traps and all epigaeic species from the pitfall traps were retained in all analyses, including rare species (those collected in only one sample). Although rare species have little impact on the community level analysis they are the species that are likely most threatened with local extinction as a result of forestry practices (Siitonen and Martikainen 1994).

Two-factor ANOVA was used to compare the number of epigaeic beetles collected in each treatment and among the two pitfall traps within sites (Trap A and Trap B). The independent variables were treatment and trap, and the dependant variable was the number of beetles. Tukey *post hoc* tests were used to compare treatments and traps.

To correct for uneven catch rates, rarefaction, a method of estimating the number of species expected in a sub-sample drawn randomly from a larger sample (Magurran 1988), was used to compare species richness using EstimateS (Colwell 1997). Separate rarefactions were conducted for epigaeic and saproxylic beetle catches using data from each of the 3 treatments.

Community structure was compared among forest cover types, tree species and mortality agents using a non-metric multidimensional scaling (NMS) ordination as implemented by PCOrd (McCune and Medford 1999). Ordinations were used to determine whether groups of beetles were associated with a specific treatment. Ordinations describe complex systems with multiple variables as a smaller set of summary variables corresponding to position along ordination axes. NMS ordination was chosen over other ordination techniques because it is well suited for arthropod community analysis and avoids the assumption of linear relationships among variables (Clarke 1993).

The stress in an ordination is crucial to its final configuration. NMS uses pair-wise comparisons to find the distance between all the points in the ordination. Distances are ranked from smallest to largest. The ordination solution is then plotted against the initial ranked real distance. Stress is the measure of the departure of the ordination solution to the original ranked distances or the departure from monotonicity. Clarke (1993) (adapted by McCune and Grace (2002)) interprets a stress <5 to be an excellent representation with no prospect for misinterpretation, ≤ 10 as a good ordination with no real risk of drawing false inferences, and 10-20 as a possibly useful picture, although values at the upper end have the potential to mislead.

The final ordination was performed with the “slow and thorough” autopilot feature in PCOrd using the Sorensen (Bray-Curtis) distance measure. The autopilot feature uses a random number generator to generate a starting configuration and performs up to 400 iterations with this starting point until an instability criterion (standard deviation of the stress over the proceeding iterations) of 0.0001 is reached. This process is repeated for a 6-dimensional to a 1-dimensional configuration. The whole process is then repeated 40 times with real data, with different starting configurations. Fifty additional randomized runs are made, shuffling the data within columns (species) between each run and using different random starting configurations. The ‘best’ configuration, defined as the one with the lowest stress, is then selected for each dimensionality. The final dimensionality of the ordination is selected when additional axis do not lower the stress by 5 or more. This final dimensionality and configuration is accepted as significant if the final stress is lower than that of 95% of the randomized runs using a Monte Carlo test.

Indicator species analysis (Dufrene and Legendre 1997) was used to detect and describe the relative importance of different beetle species in differentiating treatments. This analysis was performed using PCord (Colwell 1997) which combines the relative abundance and the relative frequency of a species into an indicator value between 0 (no indication) and 100 (perfect indication). Indicator values were then evaluated against a Monte-Carlo test statistic.

Results

Epigaeic Beetles. A total of 3019 epigaeic beetles representing 61 species and 6 families were collected using pitfall traps (Appendix A). According to life history data, 216 beetles were removed from analysies, as they were likely tourists on the forest floor (*e.g.*, Scolytidae) or it was not possible to accurately identify them to species (Aleocharinae). The two most common families were ground beetles (Carabidae) and rove beetles (Staphylinidae) which made up 76% and 20% of the total relative abundance and consisted of 22 and 31 species, respectively.

Rarefaction estimates of species richness indicate that species accumulation curves are similar for all three burn treatments (Fig. 3-1). Although it is clear that these curves have not approached asymptotes, they are extended long past inflection points suggesting that a majority of the species present in each treatment were collected. The greatest number of both species (Fig. 3-2) and individual beetles (Fig. 3-3) were collected in the light burns. Most species were shared among all treatments and 8-13 % of species within a treatment were unique to that treatment (Fig. 3-2). There was a significant difference in the average catch of epigaeic beetles among treatments ($F_{2, 18}$=4.34, P=0.03). Tukey's *post hoc* test demonstrates that the skips collected significantly fewer beetles than the light burn areas (P=0.03) (Fig. 3-3). There was no significant difference in catches between trap A (on scorched ground) and trap B (non-scorched ground) in the light burn.

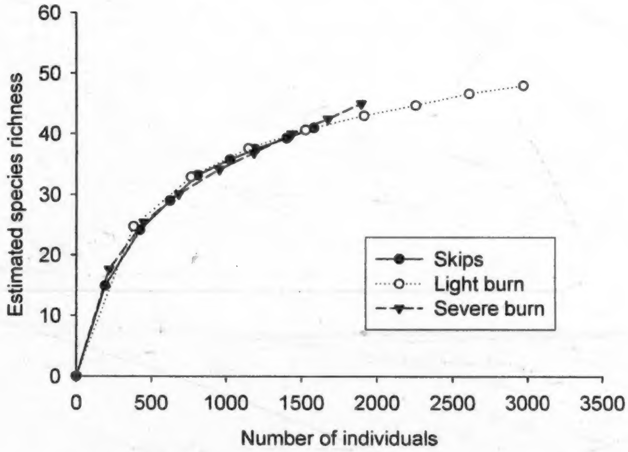

Figure 3-1 Rarefaction estimates of species richness of epigaeic beetles in sub-samples of increasing size in skips, light burns and severe burns.

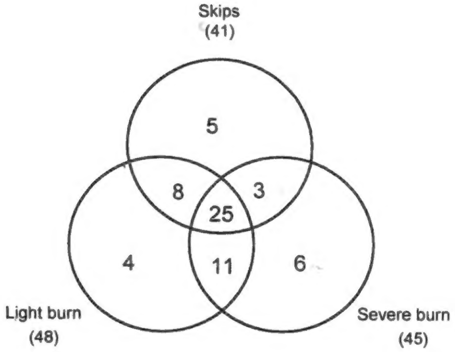

Figure 3-2 Venn diagram showing number of unique and shared species of epigaeic beetles among skips, light burns, and severe burns. Numbers in parentheses indicate total species richness for each treatment.

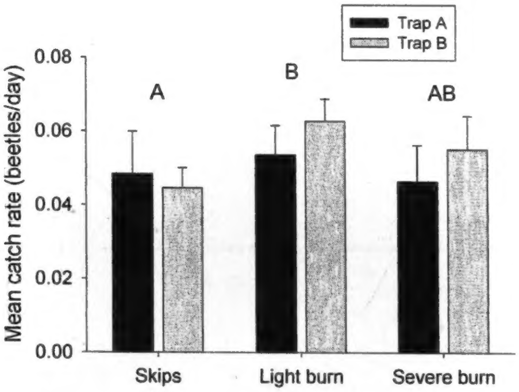

Figure 3-3 Catch of epigaeic beetles standardized to beetles per trap day in skips, light burns and severe burns. Catch for each treatment is divided into Trap A and Trap B. In light burns, Trap A was placed on scorched ground and Trap B was placed in the litter. Error bars represent one SE above the mean. Total catch (both traps combined) was compared among burn intensities using Tukey's *post hoc* tests, and pairs of bars with the same letter written above indicate no significance at alpha = 0.05.

An NMS ordination of these data (Fig. 3-4) resulted in a 2-dimensional configuration and a stress of 11, which was significantly different than randomized data using a Monte Carlo test (P<0.02). Axes 1 and 2 explains 29% and 63% of the variance, respectively, therefore, 92% of total variance is explained by this ordination. There is clear evidence for both burn treatment and temporal patterns in the data. Axis 2 clearly separates samples according to burn intensity. Axis 1 indicates some temporal separation of data, most notably for the severe burns. Species indicator analysis revealed 16 species to be closely associated with different treatments (Table 3-1). All but one of those species, *Pterostichus brevicornis* Kirby, are associated with the light or severe burns, indicating that many species have a strong affinity for burned areas. Two known pyrophilous species significantly associated with severe burns are *Sericoda quadripunctata* (De Geer) and *Sericoda bembidioides* Kirby. Interestingly the catch of both these species was higher during the first year after the burn (2000) and *S. bembidioides* was virtually non-existent the second year following burn (2001) (Fig. 3-5).

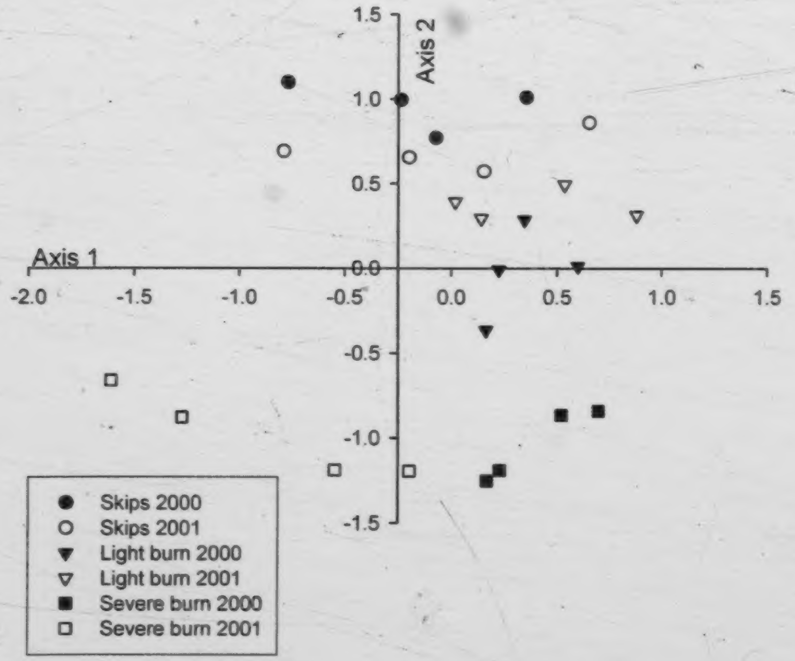

Figure 3-4 NMS ordination of epigaeic beetles in skips, light burns and severe burns. Scores are pooled samples from each treatment and replicate.

Table 3-1 Species of epigaeic beetles of significant indicator value for each treatment in a prescribed burn.

Family	Species	Total catch (Beetles/Day)	Treatment	Observed indicator value	Indicator value from randomized tests	
					Mean± SD	P
Carabidae	*Sericoda quadripunctata* (DeGeer)	5.80	Severe burn	73.2	40.4±9.52	0.002
Carabidae	*Pterostichus adstrictus* Eschscholtz	4.50	Light burn	66.2	45.9±7.21	0.004
Staphylinidae	*Quedius simulator* Smetana	0.46	Severe burn	64.8	37.5±8.38	0.003
Staphylinidae	*Quedius rusticus* Smetana	0.52	Light burn	60.6	34.1±9.27	0.018
Carabidae	*Calathus ingratus* Dejean	0.72	Light burn	59.4	39.3±6.89	0.013
Carabidae	*Pterostichus brevicornis* (Kirby)	0.11	Skip	57	21.2±9.3	0.008
Staphylinidae	*Tachyporus borealis* Campbell	0.08	Light burn	55.1	21.5±9.57	0.008
Nitidulidae	*Epuraea linearis* Mäklin	0.16	Light burn	54.2	28.1±9.34	0.025
Staphylinidae	*Staphylinus pleuralis* LeConte	2.33	Light burn	53.8	41.3±4.66	0.01
Carabidae	*Sericoda bembidioides* Kirby	1.10	Severe burn	53.2	27.8±10.62	0.033
Staphylinidae	*Acidota crenata* (Fabricius)	0.27	Severe burn	52.9	27.1±8.94	0.021
Byrrhidae	*Byrrhus cyclophorus* Kirby	0.51	Severe burn	52.4	29.7±9.99	0.042
Carabidae	*Stereocerus haematopus* (Dejean)	4.85	Light burn	51.5	40.1±5.46	0.032
Carabidae	*Carabus chamissonis* Fischer von Waldheim	0.20	Light burn	47.6	25.1±9.84	0.04
Carabidae	*Elaphrus americanus* Dejean	0.13	Severe burn	46.1	20.1±9.4	0.025
Staphylinidae	*Quedius frigidus* Smetana	0.07	Severe burn	45.3	22.4±8.72	0.048

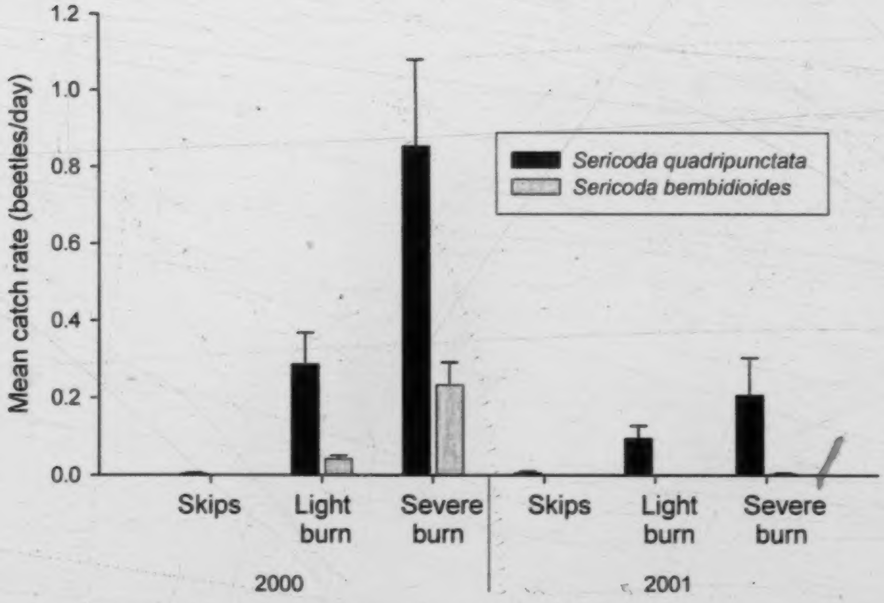

Figure 3-5 Mean standardized catch of *Sericoda quadripunctata* and *Sericoda bembidioides* one and two years following fire in skips, light burns, and severe burns. Error bars represent one standard deviation above the mean.

An additional ordination was performed on data for both years combined (Fig. 3-6), to determine whether there is a relationship between trap placement and beetle assemblage structure within the light burn. The NMS ordination, with a 2-dimensional configuration and a mean stress of 19, showed that traps placed in the duff (Trap A) occupied ordination space close to skips and traps placed where the duff was burned off (Trap B) formed a more compact and distinct cluster intermediate between skips and high intensity burns.

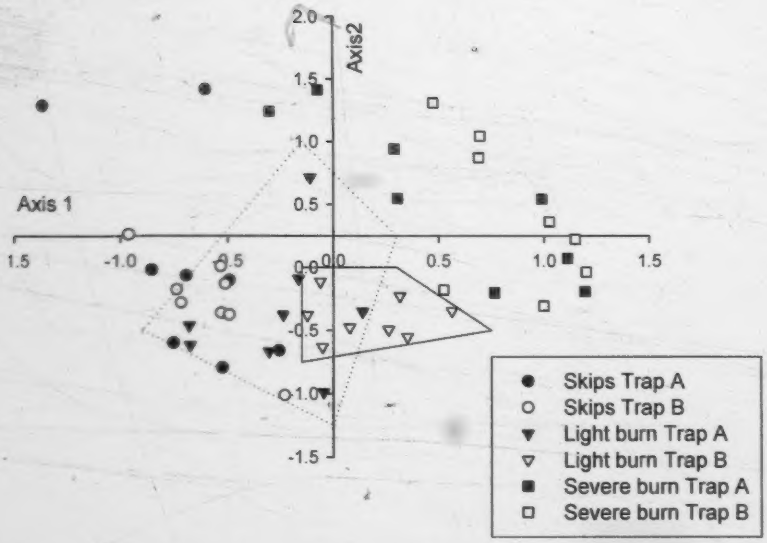

Figure 3-6 NMS ordination of epigaeic beetles in individual traps (2000 & 2001 data combined) in skips, light burns and severe burns. In light burns, Trap A (dotted polygon) was placed in duff and Trap B (solid polygon) was placed in scorched ground.

Saproxylic Beetles. A total of 10,189 beetles were collected in window traps, and 237 beetles were removed from the data set as they were not saproxylic (*e.g.*, Chrysomelidae) or they could not be accurately identified to species (*e.g.*, Aleocharinae). The analyzed dataset consisted of 9952 beetles, representing 130 species (Appendix B).

As for epigaeic species, rarefaction estimates of saproxylic species richness indicate that species accumulation curves are similar for all three treatments, although species richness was slightly higher in severe burns (Fig. 3-7). Severe burns had 32% and 38 % more species than light burns and skips, respectively, and three times as many unique species (Fig. 3-8). A large proportion of species were shared among all three treatments.

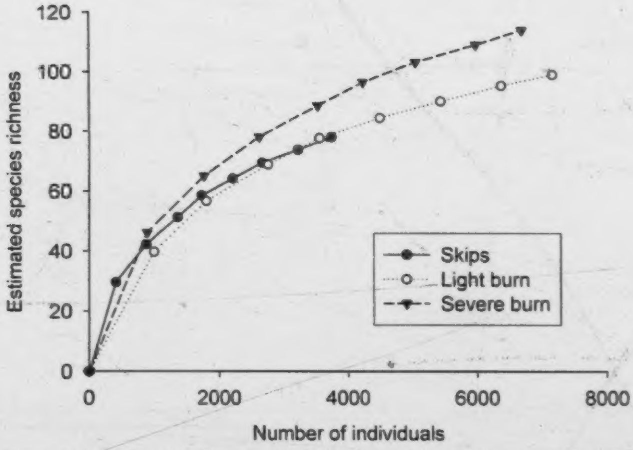

Figure 3-7 Rarefaction estimate of species richness of saproxylic beetles in subsamples of increasing size in skips, light burns and severe burns.

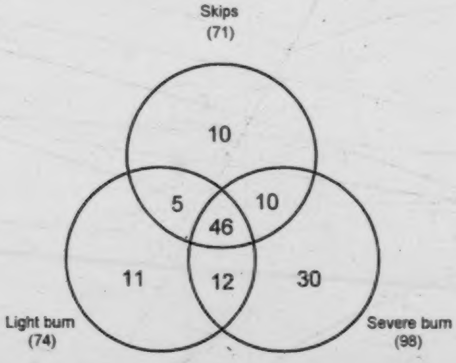

Figure 3-8 Venn diagram showing unique and shared species of saproxylic beetles in skips, light burns and severe burns. Numbers in parentheses indicate total species richness for each treatment.

The NMS ordination performed on the entire saproxylic data set produced a significant 2-dimensional ordination with a stress of 13 (Fig. 3-9). Axes 1 and 2 explain 17.5% and 65.3% of the variance, respectively. The ordination did not show any obvious groupings associated with treatment (not shown), however, there was excellent separation along Axis 1 based on year of collection (Fig. 3-9). Thus, additional NMS ordinations were performed using data from individual year of collection, and these resulted in some meaningful groupings based on burn intensity and cause of tree death.

Year-specific ordinations resulted in configurations with a mean stress of 12 and 10 for 2000 and 2001, respectively, indicating that these are useful representations of the data (Fig. 3-10 A, B). In these ordinations, each data point represents a single window trap on a tree killed by girdling or killed naturally before the stand was burned. In the first year following the fire there is a significant 2-dimensional ordination with Axes 1 and 2 explaining 64.4% and 25.1% of the variance, respectively (Fig. 3-10A). In this ordination, beetle assemblages of the severe burns clustered relatively distinctly and, within this grouping, girdled and naturally dead trees clustered separately. Traps on trees in skips and light burns did not form any distinct clusters, although traps on girdled and naturally dead trees in skips were quite different. Thus, the time since death seemed to influence assemblage structure in skips and severe burns.

In the second year following fire, NMS resulted in a significant 2-dimensional ordination with Axes 1 and 2 explaining 14.5% and 74.3% of the variance, respectively (Fig. 3-10B). In this ordination, beetle assemblages in severe burns still formed a cluster, but not quite as distinctly as in 2000. Furthermore, in 2001, there was some clustering according to cause of tree mortality within each of the treatments and overall. Overall, traps on naturally dead trees generally clustered in the lower left of the ordination space and the traps on girdled trees were spread thoughout the rest of the ordination space. Interestingly, this ordination also suggests some dissimilarity of beetle assemblages on girdled trees between severe burns and skips, with girdled trees on light burns somewhat intermediate.

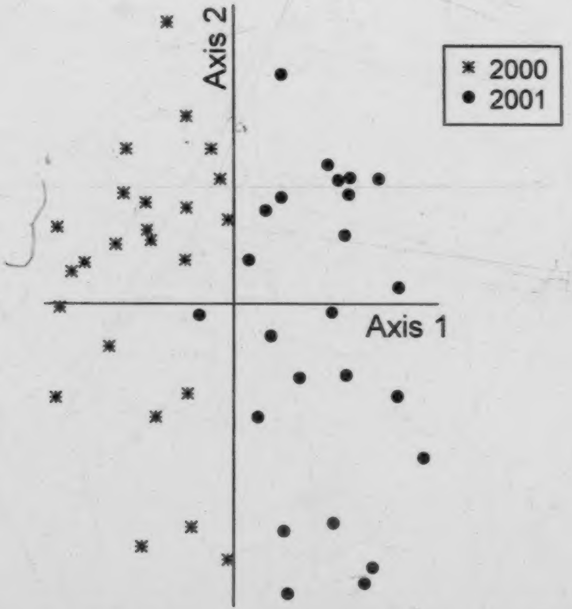

Figure 3-9 NMS ordination of saproxylic beetles in a burned coniferous stand. Points represent traps on individual trees separated by year of catch.

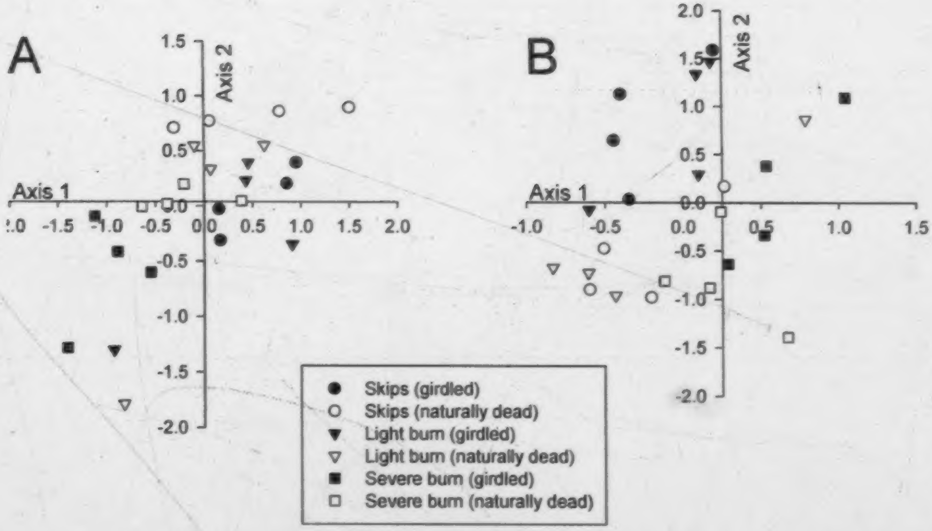

Figure 3-10 NMS ordination of saproxylic beetles in skips, light burns and severe burns: A) first year following fire (2000), and B) second year following fire (2001). Each point represents a single window trap on either a tree killed by girdling or killed naturally before the stand was burned.

Indicator analysis of saproxylic beetles showed that no species were consistent indicators of burn intensity treatment or cause of tree mortality for both years (Table 3-2). In the first year following fire, 8 species in 7 families were significant indicators of severe burns. In the second year following fire, 4 species in 4 families were significant indicators of severe burns and 2 scolytid species were indicators of skips (Table 3-2). *Xylita laevigata* (Hellenius) was an indicator of naturally killed trees in the first year and 5 species, all scolytids and their predators, were indicators of girdled trees in the second year.

Additional ordinations were performed to compare catches among traps on dead, girdled and scorched trees in the light and severe burn areas, but no consistent trends were observed. There were also no consistent differences in catch of beetles collected on these different of tree types.

Table 3-2 Species of saproxylic beetles of significant indicator value for each burn severity treatment and for cause of tree mortality (girdled or naturally dead before burning) in a prescribed burn.

Year	Family	Species	Total catch (beetles/day)	Treatment or cause of mortality	Observed indicator value	Indicator value from randomized tests	
						Mean± SD	P
2000	Corylophidae	*Molamba obesa* Casey	9.99	Severe Burn	70.2	45.1±6.35	0.001
2000	Curculionidae	*Pissodes rotundatus* LeConte	0.19	Severe Burn	61.5	24±8.98	0.002
2000	Scolytidae	*Scierus pubescens* Swaine	0.95	Severe Burn	63.3	32.6±8.56	0.005
2000	Carabidae	*Sericoda quadripunctata* (DeGeer)	0.51	Severe Burn	65.2	26.4±10.14	0.007
2000	Cucujidae	*Pediacus fuscus* Erichson	0.72	Severe Burn	69.6	29.4±11.29	0.009
2000	Cerambycidae	*Acmaeops proteus proteus* (Kirby)	0.16	Severe Burn	50	17.6±8.72	0.024
2000	Cerambycidae	*Pogonocherus penicillatus* LeConte	0.16	Severe Burn	50	18.8±9.47	0.024
2000	Cleridae	*Thanasimus undatulus* (Say)	1.33	Severe Burn	65.6	40.3±10.51	0.025
2000	Melandryidae	*Xylita laevigata* (Hellenius)	0.37	Dead Trees	55.9	55.9±6.1	0.017
2001	Melandryidae	*Xylita laevigata* (Hellenius)	0.37	Severe Burn	67	27.5±9.07	0.002
2001	Lathridiidae	*Melanophthalma villosa* (Zimmermann)	0.30	Severe Burn	69	30.7±10.55	0.006
2001	Scolytidae	*Dendroctonus rufipennis* (Kirby)	0.21	Skips	62.5	36.8±10.59	0.016
2001	Scolytidae	*Xylechinus montanus* Blackman	0.17	Skips	53.6	25.4±9.65	0.016
2001	Staphylinidae	*Acidota crenata* (Fabricius)	0.11	Severe Burn	50	17.7±8.64	0.019
2001	Scolytidae	*Dryocoetes autographus* (Ratzeburg)	1.65	Severe Burn	51.7	38.3±6.92	0.039
2001	Colydiidae	*Lasconotus* complex LeConte	0.27	Girdled Trees	59.9	31.1±8.8	0.013
2001	Scolytidae	*Crypturgus borealis* Swaine	3.32	Girdled Trees	65.6	35.9±10.34	0.018
2001	Cleridae	*Thanasimus undulatus* (Say)	1.00	Girdled Trees	54.1	29.2±8.67	0.022
2001	Scolytidae	*Dryocoetes affaber* (Mannerheim)	9.62	Girdled Trees	86.3	62.1±10.63	0.024
2001	Scolytidae	*Polygraphus rufipennis* (Kirby)	1.13	Girdled Trees	64.7	42.5±11.6	0.03

Discussion

Pyrophilous species

Species indicator analysis of epigaeic beetles revealed that 7 carabid and 6 staphylinid species were attracted to the burned sites. Comparison of these data to epigaeic beetle collections from nearby harvested treatments (Work et al., unpublished data) demonstrated that only two carabids, *Sericoda quadripunctata* and *Sericoda bembidioides*, were absent from other disturbed habitats and were, therefore, clearly pyrophilous. These two species have been previously categorized as pyrophilous, as have two other species of *Sericoda* present in Canada: *S. bogemannii* (Gyllenhal) and *S. obsoleta* (Say) (Lindroth 1961, Holliday 1984, 1991, 1992). The remaining 11 species found to be significant indicators of burned areas in this study were also abundant in harvested stands suggesting that they are disturbance-adapted species rather than fire specialists. Holliday (1984) also found general disturbance-adapted beetles common in burned stands. These beetles flourish in disturbed areas, likely due to altered microclimate, availability of mineral soils, or decreased competition (Danks and Foottit 1989).

Species indicator analysis of saproxylic beetles found 8 and 4 beetle species to be significant indicators of high intensity burns in the first and second years following fire, respectively. Comparison of these data to saproxylic beetles collected in surrounding harvested treatments (Chapter 4) shows that only *S. quadripunctata* can be considered truly pyrophilous. Thus, this species was included in analyses of both epigaeic and saproxylic data sets and was found to be indicative of burns in both sets of analyses. The other 11 saproxylic species that were strongly associated with fire in this study are not generally attracted to burned areas; however, there must be specific features (*e.g.*, large increase in coarse woody debris (CWD)) that must be present in high intensity burned areas that attract these beetles.

In contrast, Wikars (1992) found 10 saproxylic insect species, 6 of which were beetles, to be pyrophilous from flight-intercept traps in Fennoscandia. *Sericoda quadripunctata* was collected from both studies. *Henoticus serratus* was also collected from both studies, but was not significantly indicative of burned areas in my research as it was collected in the fire skips, harvested and control stands. The four other species Wikars (1992) collected were not collected in this study.

There has been comparatively little work on saproxylic beetles in forests in Canada and there is a dearth of information about habitat preferences. Evans (1966, 1971) identified the saproxylic buprestid, *Melanophila acuminata* de Geer as a true pyrophilous species. This species has a special sensory apparatus that allows it to detect smoke and heat from burning forests (Evans and Kuster 1980). Evans (1971) recognized two major groups of pyrophilous insects: 1) platypezid and empidid smoke flies and 2) some cerambycid and buprestid beetles.

The habitat parameters that make recently burned stands attractive to certain species have been an issue of speculation but not one of concerted study. Wikars (1992) stated that wildfire alters beetle assemblages by increasing the amount of CWD, changing the decay rate of CWD and by creating a temporary competition-free environment. Another possible function of insects congregating in burned areas is to act as a swarming location to find mates (Evans, 1971). Although the pyrophilous nature of *Sericoda* spp. has been known for decades, it is unknown how these beetles detect recently burned stands, nor which characteristics of burned habitats are Esseential for their success (foraging and reproduction). Wikars (1995) reported that clear-cutting before burning prevents the establishment of *S. quadripunctata*, suggesting that this species needs the large amount of burned CWD created after a wildfire that is not present after burning a clear-cut. Furthermore, it was clear that CWD quality was the most important factor affecting saproxylic beetle assemblages two years after the fire. Another certainty is that burned habitats are suitable for *Sericoda* for only 1-2 years. *Sericoda* were collected in greatest numbers in the first year following the burn and declined in abundance by the second year, a pattern also observed by Holliday (1984, 1991, 1992). Therefore, CWD qualities are important in determining beetle assemblages following wildfire, but faunal succession occurs very rapidly.

Faunal variation and succession

Both epigaeic and saproxylic beetles were collected in greater numbers in the burned patches than in the skips. Epigaeic beetles were most abundant and diverse in light burns, possibly because traps were placed in two distinct habitats (burned and unburned) on the forest floor, allowing collection of beetles favouring both by unburned conditions (*e.g.*, *Pterostichus brevicornis*) and burned areas (*i.e.*, pyrophilous species and open habitat specialists). Saproxylic beetles, in contrast, did not exhibit the same pattern of response as the light and severe burns produced similar catches of beetles, therefore maybe demonstrating habitat preference on a larger scale.

Two years after the fire, the main factor affecting saproxylic beetle assemblage composition in all treatments was time since death. The girdled trees all had similar beetle assemblages characterized by a few scolytid species and their specialized predators. The predominance of these species in the second year likely reflects emergence of the new generation of beetles following reproduction within snags after they were attacked in the first year. The beetle fauna sampled in girdled trees represents an early successional fauna that is dominated by both species that require fresh phloem and cambium for feeding and reproduction, and their respective predators. This fauna is unique to newly dead wood and is temporally restricted (1-4 years) (Hammond et al. 2001, Hammond et al. 2004). Trees dead before the fire had a highly variable beetle assemblage, possibly reflecting, to some extent, a high variability in their state of decay (*i.e.*, time since death) (Hammond et al. 2004).

Likewise, my data show distinct changes in both epigaeic and saproxylic beetles communities the second year following fire compared to the first year following fire. The change in the epigaeic beetle assemblage is most evident in the severe burn intensity class with a dramatic loss of the pyrophilous beetles (especially *S. quadripunctata* and *S. bembidioides*) that dominated the burned areas during the first year following fire. Annual variation in the saproxylic beetle community was more dramatic than in the epigaeic community, with virtually every trap having a completely different assemblage of beetles the second year following fire compared to the first year. The reason for this drastic change is likely due to the initial rapid colonization of the CWD by pyrophilous and disturbance-adapted species, and the replacement of these species with secondary colonization of the subsequently altered CWD by beetles that either are slower dispersers, or require initial attack by other species before they are able to inhabit the CWD.

Management Implications

It is clear from this study and others (Hammond et al. 2001, Siitonen 2001, Hammond et al. 2004) that there is an initial wave of beetles that colonize burned areas. This community is made up of species that are either fire-adapted or more generally disturbance-adapted. It is largely unclear in current literature exactly what role fire-adapted species play in forest processes such as decomposition and nutrient cycling. In a strict conservation sense, existing data suggest that fires have to be maintained at frequent intervals on the landscape in order to conserve these fire-adapted species. In a management sense these insects may thus play important roles in the recovery of these disturbed areas to return them to pre-disturbance. As Aldo Leopold (1966) wrote:

> "If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

Until we fully understand the roles of these beetles, and if we are trying to emulate natural processes with our forest harvesting, it is important to try and keep these beetles in our forested landscape, and incorporate them into sustainable forest management plans.

Literature Cited

Arnett, R. H. J., and M. C. Thomas. 2001a. American beetles v. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, Florida.

Arnett, R. H. J., and M. C. Thomas. 2001b. American beetles v. 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, Florida.

Bousquet, Y. 1991. Checklist of beetles of Canada and Alaska. Agriculture Canada, Ottawa, Ont.

Clark, J. S. 1990. Twentieth century climate change, fire suppression, and forest production in northwestern Minnesota. Canadian Journal of Forest Research **20**:219–232.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Colwell, R. K. 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Danks, H. V., and R. G. Foottit. 1989. Insects of the boreal zone of Canada. Canadian Entomologist **121**:625-690.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Evans, W. G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* de Geer (Buprestidae: Coleoptera). Ecology **47**:1061-1065.

Evans, W. G. 1971. The attraction of insects to forest fires. *in* Proceedings of the Tall Timbers Research Station, Tallahasse, Fl.

Evans, W. G., and J. E. Kuster. 1980. The infrared receptive fields of *Melanophila acuminata* (Coleoptera: Buprestidae). Canadian Entomologist **112**:211-216.

Gandhi, K. J. K., J. R. Spence, D. W. Langor, and L. E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera : Carabidae and Staphylinidae). Biological Conservation **102**:131-141.

Haeussler, S., and D. Kneeshaw. 2003. Comparing forest management to natural processes. Pages 307-368 *in* P. J. Burton, C. Messier, D. W. Smith, and W. L. Adamowicz, editors. Towards Sustainable Management of the Boreal Forest. NRC Research Press.

Hammond, H. E., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research **31**:1175-1183.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. Canadian Entomologist **129**:1009-1033.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research **34**:1-19.

Holliday, N. J. 1984. Carabid beetles (Coleoptera, Carabidae) from a burned spruce forest (*Picea* Spp). Canadian Entomologist **116**:919-922.

Holliday, N. J. 1991. Species responses of carabid beetles (Coleoptera, Carabidae) during postfire regeneration of boreal forest. Canadian Entomologist **123**:1369-1389.

Holliday, N. J. 1992. The carabid fauna (Coleoptera, Carabidae) during postfire regeneration of boreal forest - properties and dynamics of species assemblages. Canadian Journal of Zoology **70**:440-452.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation **65**:115-120.

Johnson, E. A. 1992. Fire and vegetation dynamics—studies from the North American boreal forest. Cambridge University Press, Cambridge, U.K.

Johnson, E. A., K. Miyanishi, and N. O'Brien. 1999. Long-term reconstruction of the fire season in the mixedwood boreal forest of Western Canada. Canadian Journal of Botany **77**:1185-1188.

Käila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica **29**:21-23.

Leopold, A. 1966. A Sand County almanac. *in*. Oxford University Press, New York, New York.

Lindroth, C. H. 1961. The ground beetles of Canada and Alaska: Part 2. Opuscula entomologica, supplementa **20**.

Magurran, A. E. 1988. Ecological diversity and its measurment. Princeton University Press, Princeton, New Jersey.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, OR.

McCune, B., and M. J. Medford. 1999. PCOrd software: multivariate analysis of ecological data. MJM Software. Gleneden Beach, OR.

Muona, J., and I. Rutanen. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forests. Annales Zoologici Fennici **31**:109-121.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In A systems analysis of the boreal forest. Cambridge University Press, Cambridge, U.K.

Richardson, R. J., and N. J. Holliday. 1982. Occurrence of carabid beetles (Coleoptera, Carabidae) in a boreal forest damaged by fire. Canadian Entomologist **114**:509-514.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins **49**:11-41.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russion Karelia. Scandinavian Journal of Forest Research **9**:185-191.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe Publications, Strasbourg.

Spence, J. R., and J. K. Niemelä. 1994. Sampling carabid beetle assemblages with pitfall traps: the madness and the method. Canadian Entomologist **126**:881-894.

Wikars, L. O. 1992. Forest fires and insects. Entomologisk Tidskrift **113**:1-11.

Wikars, L. O. 1995. Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera:Carabidae). Annales Zoologici Fennici **32**:375-384.

Wikars, L. O. 1997. Pyrophilous insects in Orsa Finnmark, central Sweden: biology, distribution, and conservation. Entomologisk Tidskrift **118**:155-169.

Wikars, L. O. 2002. Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation **6**:1-12.

Wikars, L. O., and J. Schimmel. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. Forest Ecology and Management **141**:189-200.

Work, T. T., D. P. Shorthouse, J. R. Spence, W. J. A. Volney, and D. W. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research **34**:417-430.

Appendix 3-A

Epigaeic beetles collected using pitfall traps in a prescribed burn at the EMEND research site.

Family	Species	Years collected	Fire intensity[a]
Byrrhidae	*Byrrhus cyclophorus* Kirby	2000-2001	Sk,Lb,Sb
	Simplocaria metallica (Sturm)	2000-2001	Lb,Sb
Carabidae	*Agonum retractum* LeConte	2000-2001	Lb,Sb
	Bembidion grapii Gyllenhal	2000-2001	Lb,Sb
	Bembidion incertum (Motschulsky)	2000	Sb
	Bembidion rupicola (Kirby)	2000	Sb
	Bembidion transparens (Gebler)	2000	Sb
	Calathus advena (LeConte)	2000-2001	Sk,Lb,Sb
	Calathus ingratus Dejean	2000-2001	Sk,Lb,Sb
	Calosoma frigidum Kirby	2000	Sk
	Carabus chamissonis Fischer von Waldheim	2000-2001	Sk,Lb
	Elaphrus clairvillei Kirby	2000-2001	Sb
	Loricera pilicornis (Fabricius)	2000-2001	Lb,Sb
	Patrobus foveocollis (Eschscholtz)	2000-2001	Sk,Lb,Sb
	Platynus decentis (Say)	2000-2001	Sk,Lb,Sb
	Pterostichus adstrictus Eschscholtz	2000-2001	Sk,Lb,Sb
	Pterostichus brevicornis (Kirby)	2000-2001	Sk,Sb
	Stereocerus haematopus	2000-2001	Sk,Lb,Sb
	Pterostichus pensylvanicus LeConte	2000-2001	Lb,Sb
	Pterostichus punctatissimus (Randall)	2000-2001	Sk,Lb,Sb
	Sericoda bembidioides Kirby	2000-2001	Lb,Sb
	Sericoda quadripunctata (DeGeer)	2000-2001	Sk,Lb,Sb
	Trechus apicalis Motschulsky	2000-2001	Sb
Cryptophagidae	*Caenoscelis antennalis* (Casey)	2000-2001	Sk,Lb,Sb
	Cryptophagus tuberculosus Maklin	2000-2001	Sk,Lb

Family	Species	Years collected	Fire intensity[a]
Leiodidae	*Catops americanus* Hatch	2001	Sk,Lb
	Catops basilaris Say	2001	Sk
Nitidulidae	*Epuraea linearis* Mäklin	2000-2001	Sk,Lb,Sb
	Glischrochilus siepmanni W.J.Brown	2000	Lb
Staphylinidae	*Acidota crenata* (Fabricius)	2000-2001	Sk,Lb,Sb
	Acidota quadrata (Zetterstedt)	2000-2001	Sk,Lb
	Bolitobius horni Campbell	2000-2001	Sk,Lb
	Deinopteroloma subcostatum (Maklin)	2001	Lb
	Eucnecosum brunnescens (J.Sahlberg)	2001	Sk
	Gabrius brevipennis (Horn)	2000-2001	Sk,Lb,Sb
	Ischnosoma splendidum (Gravenhorst)	2000-2001	Sk,Lb,Sb
	Lathrobium fauveli Duvivier	2001	Sk
	Lathrobium washingtoni Casey	2000	Lb
	Lordithon fungicola Campbell	2000-2001	Sk,Sb
	Megarthrus sinuaticollis Boisduval & Lacordaire	2001	Lb,Sb
	Mycetoporus americanus Erichson	2000-2001	Sk,Lb,Sb
	Omalium foraminosum Maklin	2000-2001	Lb
	Pseudopsis sagitta Herman	2000	Sb
	Quedius brunnipennis Mannerheim	2000-2001	Sk,Lb,Sb
	Quedius caseyi caseyi Scheerpeltz	2000-2001	Sk,Sb
	Quedius frigidus Smetana	2000-2001	Lb,Sb
	Quedius fulvicollis (Stephens)	2000	Lb,Sb
	Quedius labradorensis labradorensis Smetana	2000-2001	Sk,Lb,Sb
	Quedius rusticus Smetana	2000-2001	Sk,Lb,Sb
	Quedius simulator Smetana	2000-2001	Sk,Lb,Sb
	Quedius transparens Motschulsky	2000	Sk,Lb
	Quedius velox Smetana	2000-2001	Sk,Lb,Sb
	Scaphium castanipes Kirby	2000-2001	Sk,Lb,Sb

Family	Species	Years collected	Fire intensity[a]
	Staphylinus pleuralis LeConte	2000-2001	Sk,Lb,Sb
	Stenus austini Casey	2001	Sk,Lb,Sb
	Tachinus frigidus Erichson	2000-2001	Sk,Lb,Sb
	Tachinus fumipennis (Say)	2000-2001	Sk,Lb,Sb
	Tachinus quebecensis Robert	2000-2001	Sk,Lb
	Tachyporus borealis Campbell	2000	Sk,Lb
	Tachyporus borealis Campbell	2000-2001	Sk

[a] Sk-skips, Lb-light burn, Sb-Severe burn

Appendix 3-B

Saproxylic beetles collected by flight intercept traps in a prescribed burn at the EMEND research site.

Family	Species	Years collected	Treatment[a]	Tree type[b]
Anobiidae	*Ernobius* sp.	2001	Sb	G
	Hemicoelus carinatus (Say)	2000-2001	Lb	S
	Microbregma emarginatum emarginatum (Duftschmid)	2000-2001	Sk,Lb,Sb	G,D,S
	Ptilinus lobatus Casey	2000-2001	Lb,Sb	G,S
	Utobium elegans (Horn)	2000-2001	Sk,Lb,Sb	G,D,S
Bostrichidae	*Rhyzopertha dominica* (Fabricius)	2001	Sb	D
	Stephanopachys sp.	2000	Lb,Sb	S
Buprestidae	*Anthaxia inornata* (Randall)	2000-2001	Sb	G,S
	Buprestis maculativentris Say	2000-2001	Sb	S
	Dicerca tenebrosa (Kirby)	2000-2001	Lb,Sb	G,D,S
	Melanophila acuminata (DeGeer)	2000	Sb	S
	Melanophila fulvoguttata (Harris)	2001	Sk	G
Cantharidae	*Dichelotarsus piniphilus* (Eschscholtz)	2000	Sk,Lb,Sb	G,D,S
Carabidae	*Agonum consimile* (Gyllenhal)	2001	Sb	D
	Amara aeneopolita Casey	2000-2001	Sk,Sb	G
	Bembidion grapii Gyllenhal	2000-2001	Lb,Sb	S
	Bembidion rupicola (Kirby)	2000	Lb	G,S
	Bembidion timidum (LeConte)	2000	Sb	D
	Bradycellus lecontei Csiki	2001	Sb	D
	Calathus advena (LeConte)	2000-2001	Sk,Lb,Sb	G,D,S
	Calosoma frigidum Kirby	2001	Lb	S
	Dicheirotrichus cognatus (Gyllenhal)	2000-2001	Sb	G,D
	Pterostichus adstrictus Eschscholtz	2000	Lb,Sb	S
	Sericoda bembidioides Kirby	2000	Lb,Sb	G,D,S
	Sericoda quadripunctata (DeGeer)	2000-2001	SkLb,Sb	G,D,S
Cerambycidae	*Acmaeops proteus proteus* (Kirby)	2000-2001	SkLb,Sb	G,D,S

Family	Species	Years collected	Treatment[a]	Tree type[b]
	Arhopalus foveicollis (Haldeman)	2000-2001	Sk,Lb,Sb	G,D,S
	Asemum striatum (Linné)	2000-2001	Lb,Sb	G,S
	Meriellum proteus (Kirby)	2000	Lb	S
	Monochamus scutellatus scutellatus (Say)	2000-2001	Lb,Sb	G,S
	Pachyta lamed liturata Kirby	2001	Lb	S
	Phymatodes dimidiatus (Kirby)	2000-2001	Lb,Sb	G,S
	Pogonocherus penicillatus LeConte	2000-2001	Lb,Sb	G,D,S
	Rhagium inquisitor (Linné)	2000-2001	Sb	G,S
	Spondylis upiformis Mannerheim	2000-2001	Sk,Lb,Sb	G,D,S
	Tetropium parvulum Casey	2001	Lb	S
	Xylotrechus undulatus (Say)	2001	Sk	D
Cerylonidae	*Cerylon castaneum* Say	2000	Sk,Lb,Sb	G,D,S
Ciidae	*Cis fuscipes* Mellié	2000-2001	Sk,Lb,	G,D
	Cis sp.	2000	Sb	D
	Dolichocis manitoba Drury	2000-2001	Sk,Lb,Sb	D,S
	Sulcacis curtula (Casey)	2000	Lb	S
Clambidae	*Clambus pubescens* Redtenbacher	2000-2001	Sk,Lb,Sb	G,D,S
Cleridae	*Thanasimus dubius* (Fabricius)	2000	Sk,Lb,Sb	G,D,S
	Thanasimus undulatus (Say)	2000-2001	Sk,Lb,Sb	G,D,S
Colydiidae	*Lasconotus complex* LeConte	2000-2001	Sk,Lb,Sb	G,D,S
Corylophidae	*Molamba obesa* Casey	2000-2001	Sk,Lb,Sb	G,D,S
Cryptophagidae	*Atomaria* spp.	2001	Sk,Lb,	D,S
	Caenoscelis antennalis (Casey)	2000-2001	Sk,Lb,Sb	G,D,S
	Cryptophagus tuberculosus Mäklin	2000-2001	Sk,Sb	G,D
	Cryptophagus varius Woodroffe & Coombs	2000-2001	Sk,Lb,Sb	G,D,S
	Henoticus serratus (Gyllenhal)	2000	Sk,Lb,Sb	G,D,S
Cucujidae	*Cucujus clavipes clavipes* Fabricius	2000-2001	Sk,Lb,Sb	G,D,S
	Dendrophagus cygnaei Mannerheim	2000-2001	Lb,Sb	G,D,S

Family	Species	Years collected	Treatment[a]	Tree type[b]
	Pediacus fuscus Erichson	2000-2001	Lb,Sb	G,D,S
Curculionidae	*Hylobius congener* Dalla Torre,Schenkling,Marshal	2000	Sb	D
	Hylobius pinicola (Couper)	2000	Lb	G
	Pissodes rotundatus LeConte	2000-2001	Sk,Lb,Sb	G,D,S
	Rhyncolus brunneus Mannerheim	2000-2001	Sk,Lb,Sb	G,D,S
Elateridae	*Ampedus miniipennis* (LeConte)	2001	Sb	D
	Ctenicera resplendens (Eschscholtz)	2000	Lb,Sb	G,S
Eucnemidae	*Epiphanis cornutus* Eschscholtz	2001	Sb	D
	Hylis terminalis (LeConte)	2000	Lb	S
Histeridae	*Hister* sp.	2000-2001	Sk,Lb,Sb	G,D,S
Lathridiidae	*Cartodere constricta* (Gyllenhal)	2001	Lb,Sb	G,S
	Corticaria serrata (Paykull)	2000-2001	Sk,Lb,Sb	G,D,S
	Corticaria sp. A	2000	Sb	S
	Corticaria sp. B	2000	Sk,Lb,SbSb	D,S
	Enicmus mimus Fall	2000	SbSb	D,S
	Enicmus tenuicornis LeConte	2001	Sk	D
	Lathridius minutus (Linné)	2000-2001	Sk,Lb,Sb	G,D,S
	Melanophthalma villosa (Zimmermann)	2000-2001	Sk,Lb,Sb	G,D,S
Leiodidae	*Agathidium* sp.	2000-2001	Sb	G,D,S
Melandryidae	*Enchodes sericea* (Haldeman)	2000	Sk	G
	Serropalpus substriatus Haldeman	2001	Lb,Sb	G,S
	Xylita laevigata (Hellenius)	2000-2001	Sk,Lb,Sb	G,D,S
	Xylita livida (C.R.Sahlberg)	2000-2001	Sb	S
	Zilora hispida LeConte	2000	Sb	D
Micropeplidae	*Micropeplus laticollis* Mäklin	2001	Sk	G
Nitidulidae	*Epuraea linearis* Mäklin	2000-2001	Sk,Lb,Sb	G,D,S
	Glischrochilus moratus W.J.Brown	2000	Sb	D
	Glischrochilus sanguinolentus sanguinolentus (Olivier)	2000	Sk,Lb,Sb	G,D,S

Family	Species	Years collected	Treatment[a]	Tree type[b]
	Glischrochilus siepmanni W.J.Brown	2000	Lb	D
	Glischrochilus vittatus (Say)	2000-2001	Sk,Lb,Sb	G,D,S
Ptiliidae	*Acrotrichis* spp.	2000-2001	Sk,Lb,Sb	G,D,S
Pythidae	*Pytho* sp.	2000-2001	Sk,Sb	D,S
Rhizophagidae	*Rhizophagus brunneus brunneus* Horn	2000-2001	Sk,Lb,Sb	G,D,S
	Rhizophagus dimidiatus Mannerheim	2000-2001	Sk,Lb,Sb	G,D,S
	Rhizophagus remotus LeConte	2000	Lb,Sb	D,S
Scolytidae	*Carphoborus andersoni* Swaine	2000	Sb	S
	Cryphalus ruficollis Hopkins	2001	Lb,Sb	G,D,S
	Crypturgus borealis Swaine	2000-2001	Sk,Lb,Sb	G,D,S
	Dendroctonus rufipennis (Kirby)	2000-2001	Sk,Lb,Sb	G,D,S
	Dryocoetes affaber (Mannerheim)	2000-2001	Sk,Lb,Sb	G,D,S
	Dryocoetes autographus (Ratzeburg)	2000-2001	Sk,Lb,Sb	G,D,S
	Ips pini (Say)	2000-2001	Sk,Lb,Sb	G,D,S
	Phloeotribus prob.*lecontei* Schedl	2000	Sk,Sb	D
	Pityogenes plagiatus plagiatus (LeConte)	2000	Sk,Sb	G,D
	Pityokteines ornatus (Swaine)	2001	Lb,Sb	G,D
	Pityophthorus sp.	2000	Sb	G
	Polygraphus rufipennis (Kirby)	2000-2001	Sk,Lb,Sb	G,D,S
	Scierus annectans LeConte	2000-2001	Sk,Lb,Sb	G,D,S
	Scierus pubescens Swaine	2000-2001	Sk,Lb,Sb	G,D,S
	Trypodendron lineatum (Olivier)	2000-2001	Sk,Lb,	G,D,S
	Trypodendron retusum (LeConte)	2000-2001	Sk,Lb,Sb	G,D,S
	Trypodendron rufitarsis Kirby	2000	Lb,Sb	G,D,S
	Xylechinus montanus Blackman	2000-2001	Sk,Lb,Sb	G,D,S
Staphylinidae	*Acidota crenata* (Fabricius)	2000-2001	Sk,Lb,Sb	G,D,S
	Acidota quadrata (Zetterstedt)	2000	Sb	G
	Anotylus sobrinus (LeConte)	2001	Lb,Sb	D

Family	Species	Years collected	Treatment[a]	Tree type[b]
	Bisnius tereus Smetana	2001	Sk,Lb,	D,S
	Gabrius brevipennis (Horn)	2000	Sk,Lb,Sb	G,D,S
	Heterothops fusculus LeConte	2000	Sb	G
	Ischnosoma splendidum (Gravenhorst)	2000	Lb	D
	Lathrobium fauveli Duvivier	2000	Lb	S
	Lordithon fungicola Campbell	2000	Sk,Lb,Sb	G,S
	Megarthrus sinuaticollis Boisduval & Lacordaire	2000-2001	Lb,Sb	G,D,S
	Nudobius cephalus (Say)	2000-2001	Sk,Lb,Sb	G,D,S
	Olisthaerus sp.	2000-2001	Lb,Sb	G,D,S
	Omalium foraminosum Mäklin	2001	Lb	S
	Phleostiba lapppnicus (Zetterstedt)	2000-2001	Sk,Lb,Sb	G,D,S
	Pseudopsis sagitta Herman	2000-2001	Sk,Lb,	G,D
	Pseudopsis sp.	2000	Lb	S
	Quedius plagiatus Mannerheim	2000-2001	Sk,Lb,Sb	D,S
	Quedius rusticus Smetana	2000-2001	Sk,Lb,Sb	G,D,S
	Quedius simulator Smetana	2000-2001	Sk,Lb,Sb	G,D
	Quedius velox Smetana	2001	Sk,Lb,Sb	G,D,S
	Staphylinus pleuralis LeConte	2000-2001	Lb	G,D
	Stenus austini Casey	2000	Lb	G
	Tachinus frigidus Erichson	2001	Lb,Sb	S

[a] Sk-skips, Lb-light burn, Sb-severe burn

[b] G-girdled trees, D-naturally dead snags, S-scorched trees

Chapter 4 Effects of Variable Retention Harvesting on Saproxylic Beetle Assemblages

Introduction

In many forest ecosystems, large and diverse communities of organisms are associated with coarse woody debris (CWD) (Alexander 1995, Siitonen 2001, Hammond et al. 2004). These organisms use CWD for food, shelter, foraging or reproductive activities (Hammond 1997). Speight (1989) called specific attention this community and defined 'saproxylic' organisms as those that depend, during some part of the life cycle, upon dead wood, wood-inhabiting fungi or the presence of other saproxylic organisms. Saproxylic organisms perform important ecosystem functions in relation to decomposition and nutrient cycling (Reichle 1977, McGill and Spence 1985, Hammond 1997, Hammond et al. 2001). Although the functional roles of saproxylic organisms are often linked to fungi, insects, particularly beetles, comprise a large part of the biodiversity associated with dead wood. As a result, saproxylic insects have become the focus of many biodiversity studies in Europe (Siitonen and Martikainen 1994, Hammond 1997, Martikainen et al. 2000, Hammond et al. 2001, Martikainen 2001, Siitonen 2001, Simila et al. 2002, Sippola et al. 2002) and are receiving increasingly more attention in North America (Hammond 1997, Hammond et al. 2001, Hammond et al. 2004).

Saproxylic organisms, especially rare and threatened species, are sensitive to anthropogenic disturbances and, in Europe, industrial forestry has been clearly implicated in biologically significant declines in diversity. In Europe, these negative effects can be more readily detected because their insect fauna is well described and intensive forestry has been occurring for much longer than in North America. For example, in Fennoscandia, Siitonen and Martikainen (1994) showed that industrial forestry was associated with extirpation or extreme reductions in population sizes of several saproxylic species. In addition, the negative effects of forest harvesting on saproxylic communities has been largely attributed to changes in the quantity and age distribution of CWD in managed stands (Siitonen 2001). In North America, the saproxylic arthropod fauna is yet too poorly studied to accurately assess the current or potential impacts of forestry. However, forest resource managers are conscious of the potential impacts of forest management on biodiversity and have begun to modify management practices to reduce potential impacts (Work et al. 2003)

Variable retention (VR) harvesting is a relatively new forest management procedure whereby varying proportions of trees are left in an area after harvesting. This idea was initially introduced in North America by the Clayquot Scientific Panel (1995) and subsequently described by Franklin et al. (1997). The main goal of VR harvesting is to leave more structure on the landscape, because the structural complexity left after natural disturbances is thought to play important roles in ecosystem function and the maintenance of biological diversity (Bunnell et al. 1999). In addition to leaving more structure on the landscape, VR harvesting will also affect CWD succession by increasing the input of CWD into these systems. If there are major benefits of VR for saproxylic assemblages, they should logically become more evident over the long term when the residual structure starts to influence CWD dynamics. However, in the interest of providing some interim direction to guide current forest management decisions, examination of the short term effects of VR harvesting can provide an early indication of the amount of residual structure required to conserve saproxylic species diversity, and whether it is more beneficial to leave this structure in dispersed or clumped patterns.

In this study, I examined the short term effects of different levels of dispersed residual structure on saproxylic beetles in white spruce dominated stands. Although the amount and diversity of CWD should be relatively unaffected by the treatments, the treatments should, however, alter microclimate and physical structure affecting dispersal resulting in changes in saproxylic beetle assembles. Because of the close association between saproxylic organisms and quality of CWD (Hammond et al. 2004), I also expected the response of saproxylic beetles to treatments to differ depending on association with CWD at different stages of decay.

Materials and Methods

Study Sites. The field aspects of this study were conducted at the Ecosystem Management by Emulating Natural Disturbance (EMEND) research site (http://www.biology.ualberta.ca/old_site/emend//index.htm). EMEND is located in the Clear Hills Upland, Lower Foothills ecoregion of northern Alberta, approximately 90km north-west of Peace River (56° 46' 13"N, 118° 22' 28"W). The elevation on the site ranges from 677m to 880m, and the soils at the site are fine-textured lacustrian (Work et al. 2004). The stands examined in this study were 80 to 140 years old and forests in this area had never before been harvested commercially.

The 15 stands studied were each *c.*10ha in size, dominated at canopy level by white spruce (*Picea glauca* (Moench) Voss), and contained a small proportion of black spruce (*Picea mariana* (Miller)) and lodgepole pine (*Pinus contorta* Dougl.). Stands of adequate size that were chosen were those most similar in age, volume and composition on the EMEND landscape. In the winter of 1998/1999, four VR harvesting treatments were applied to the sites using a uniform shelterwood system as follows: 1) 75% residual - 5m wide machine corridors spaced 20m (center-center) apart, leaving 15m wide retention corridors; 2) 50% residual, additional trees were removed from the retention corridors at a ratio of 1:3 (removed: leave standing); 3) 20% residual, trees were removed from the retention corridors at a ratio of 3:4; and 4) 10% residual, trees were removed from the retention corridors at a ratio of 7:8 (see Work et al. 2004). The experiment also contained controls (no harvesting). All treatments and controls were replicated 3 times.

Beetle Sampling. Saproxylic beetles were sampled with passive barrier (window) traps, similar to those deployed by Hammond (1997), as modified from Käila (1993). Traps consisted of a clear piece of plastic (plexiglass®), 1.5mm x 20cm x 30cm attached perpendicularly to trees to intercept insects on or near the tree. Intercepted insects then fell through a cloth funnel attached to the bottom of the interception panel, and were collected in a small plastic bag filled with ethylene glycol at the bottom of the funnel. This plastic bag was replaced with a new bag of fresh ethylene glycol every 2-3 weeks throughout the sampling period. Passive barrier traps were chosen as they are an unbiased sampling method for flying arthropods orienting to trees, snags and logs, are easy to replicate in quantity, and they provide large data sets suitable for community level statistical analysis.

Three sample sites were established randomly in each 10ha compartment, at least 50m from the edge, and two traps were placed in each of the three sites during April 2000. Two trap treatments were utilized to collect a broad range of saproxylic beetles and to examine the effects that trees at different stages of decay have on saproxylic beetles. The trap treatments were: 1) traps placed on trees killed by girdling and 2) traps placed on naturally dead white spruce snags. To kill trees, I used a hatchet to cut a band at least three inches wide to the depth of the sapwood at 50cm height along the bole. The naturally killed snags were estimated to have been dead 5-8 years and still retained most of their bark and small branches. Traps were placed on trees at approximately breast height, and sampled trees were at least 10m apart. Beetles were sampled from April to August during the summers of 2000 and 2001.

All beetles were identified in the laboratory to the lowest taxonomic level possible based on current literature and local expertise. In most cases, species-level identification was possible except for the Aleocharinae (Staphylinidae), and some genera in the Nitidulidae, Lathridiidae and Leiodidae. Family and generic nomenclature follows that of Arnett (2001a, 2001b) and species nomenclature follows that of Bousquet (1991). All beetle species were designated to a functional feeding group based on available literature regarding their feeding ecology. Synoptic collections of all beetles are deposited in the Strickland Museum, University of Alberta and the museum of the Northern Forestry Centre, Canadian Forest Service.

CWD Measurement. CWD measurements were made at both the stand level and local (*i.e.*, trap) level in 2001. Stand level downed woody debris (DWD) was measured using 18 plots per stand. In each stand, a total of six 40m transects (the center lines of previously established 2m X 40m permanent biomass plots) were used to establish DWD plots. In each stand, three transects were located near the beetle sampling sites and three were not. Three DWD plots were placed randomly along each 40m transect with a minimum of 5m between each plot. DWD plots consisted of three 5m transects radiating out from a central point on the main 40m transect, separated from each other by 120°. For each piece of DWD intercepted by the 5m transects, the diameter at the point of interception was recorded along with the decay class. Only DWD with a diameter ≥ 7.0cm at point of interception was tallied. Decay classes were divided into three categories: 1) windfall from the winter of 1999-2000; 2) windfall created from 1997 to the fall of 1999, and 3) material in advanced stages of decay (losing bark and starting to rot). Stand level volume estimates were then calculated for each DWD plot using the Van Wagner formula (Van Wagner 1968), and averaged for each stand.

Snags were assessed at the stand level by using 40m x 10m plots that overlaid the six 2 x 40m plots utilized for measuring DWD. Thus, there were 6 snag plots per stand. In each plot the number of snags was tallied and for each snag the diameter at breast height (DBH) was measured.

Local measurements of CWD consisted of measuring DBH for all snags holding traps, and circular CWD plots (5m radius) were established around each trap tree, where the number of pieces of CWD (over 8cm diameter) in each plot were counted and categorized according to the criteria listed in Table 4-1.

Table 4-1 Criteria used for classifying CWD at the local level around each trap.

Stumps (standing material >1.5m tall)		
Naturally occurring stumps		
Stumps created by harvesting		
Snags (standing material <1.5m tall)		
Decay Class (DC)	Twigs	% of stem covered in bark
1	Many	>90
2	Few or absent	60-90
3	Absent	>60
Logs (down woody material >8cm diameter)		
Decay Class (DC)	% of log covered by bark	% of log covered with plants, fungi and lichens
1	>90	<10
2	60-90	10-30
3	<60	>30

Data Analysis. Capture from each trap was standardized to abundance per day to adjust for uneven sampling effort resulting from animal disturbance of some traps. All saproxylic species were retained in all analyses, including rare species (those collected in only one sample). Although rare species have little impact on the community level analyses, they are the species that are considered to be most threatened with local extinction as a result of forestry practices (Siitonen and Martikainen 1994).

To correct for uneven catch rates, rarefaction, a method of estimating the number of species expected in a sub-sample drawn randomly from the larger sample (Magurran 1988), was used to compare species richness. Rarefaction estimates of species richness were obtained from non-standardized data for each treatment functional group combination using the EstimateS software package (Colwell 1997).

Community structure was compared among forest cover types, tree species and mortality agents using non-metric multidimensional scaling (NMS) ordination procedures in PCOrd statistical package (McCune and Medford 1999). Ordinations were used to determine whether groups of beetles were associated with a specific habitat. NMS ordination was chosen over other possible techniques because it is well suited for arthropod community analysis and avoids the assumption of linear relationships among variables (Clarke 1993).

The stress in an ordination is crucial to its final configuration and interpretation. NMS uses pair-wise comparisons to find the distance between all the points in the ordination. Distances are ranked from smallest to largest and the pair-wise distances in the ordination solution are then plotted against the initial ranked real distance. Stress is the measure of the departure of the ordination solution from the original ranked distances or the departure from monotonicity. Clarke (1993) (adapted by McCune and Grace (2002)) interprets a stress < 5 to be an excellent representation with no prospect for misinterpretation, ≤ 10 as a good ordination with no real risk of drawing false inferences, and 10-20 as a possibly useful picture, although values at the upper end have the potential to mislead.

Final ordinations were performed with the "slow and thorough" autopilot feature in PCOrd (McCune and Medford 1999) using the Sorensen (Bray-Curtis) distance measure. The autopilot feature uses a random number generator to generate a starting configuration and performs up to 400 iterations with this starting point until an instability criterion (standard deviation of the stress over the proceeding iterations) of 0.0001 is reached. This process is repeated for a 6-dimensional to a 1-dimensional configuration and then the whole process is repeated 40 times with real data using different starting configurations. Fifty additional randomized runs are made by shuffling the data within columns (species) between each run and using different random starting configurations. The 'best' configuration, defined as the one with the lowest stress, is then selected for each dimensionality. The final dimensionality of the ordination is selected when additional axes do not lower the stress by 5 or more. This final dimensionality and configuration is accepted as significant if the final stress is lower than that of 95% of the randomized runs using a Monte Carlo test.

Samples in all the ordinations are the standardized sum of the catches of three traps on naturally dead trees, or of three traps on girdled trees for each of the three replicate stands of each treatment.

Indicator species analysis (Dufrene and Legendre 1997) was used to detect and describe the relative importance of different beetle species in differentiating habitat types (cover type, tree species, cause of tree death (natural versus girdling)). This analysis was performed using PCord (McCune and Medford 1999), which combines the relative abundance and the relative frequency of a species into an indicator value between 0 (no indication) and 100 (perfect indication). Significance of indicator values was then evaluated against a Monte-Carlo test statistic.

Two-factor ANOVA was used to compare the number of pieces of CWD in the 5m radius CWD plots around each trap tree. The independent variables were treatment and CWD type, and the dependant variable was the number of pieces. Log transformation was used to improve normality of the data distribution. Tukey HSD *post hoc* tests were used to compare individual cover types and CWD types and significance was based on a rejection coefficient of 0.05.

Structural variables were compared to species assemblages using multivariate regression trees (MRT) (De'Ath 2002). MRT have been used successfully to compare insect communities with environmental factors (Work et al. 2004). MRT is a rule-based technique creating dichotomies based on environmental variables. It is a hierarchical technique where each split is chosen to minimize the dissimilarity in the sites within the clusters. Distance measure used was Sorensen (Bray-Curtis). The tree is then "pruned" based on a stopping rule to have the smallest (or close to the smallest) mean square error (Breiman et al. 1984). The data are then presented in the form of a tree with species abundance graphs illustrating changes in species assemblages. The entire saproxylic beetle community was compared to 2 categorical variables (decay stage and stand), and 55 continuous variables (harvesting intensity, DBH, live tree densities, live white spruce densities, mean stand DWD, mean stand DWD by species, mean stand DWD by decay class, stand density of snags, stand density of snags by species and counts of local CWD around each trap). MRT were computed using R package (R Development Core Team 2004).

Results

Course Woody Debris. Stand level DWD did not differ among treatments and controls for DWD species combined (ANOVA, $F_{4,20}$=0.76, P=0.57) (Fig. 4-1). There were no differences between the overall amounts of coniferous and deciduous DWD across the treatments (ANOVA, $F_{1,20}$=0.87, P=0.36) nor any significant interaction between treatments and species of tree (ANOVA, $F_{4,20}$=1.42, P=0.26) (Fig 4-1). There was a significant treatment effect on snag density (ANOVA, $F_{4,20}$=14.65, P<0.001), significant differences in the amount of coniferous and deciduous snags for all treatments (ANOVA, $F_{1,20}$=17.41, P<0.001) and a significant interaction between the treatments and snag species on density (ANOVA, $_{F2,20}$=3,90, P=0.017). *Post hoc* tests indicate that there were more coniferous snags in treatments with higher retention (Fig 4-2).

Most of the pieces of CWD within a 5m radius of each trap tree were logs in intermediate and advanced stages of decay (Logs DC1,DC2) (Table 4-2). The total number of pieces of CWD differed among treatments (ANOVA, $F_{4,80}$=88.24, P<0.01) with controls having more pieces than 75% residual (P=0.004) and 50% residual (P=0.02) treatments (Table 4-2). There was a significant interaction between the effect of treatment and the type of CWD (ANOVA, $F_{28,80}$=62.35, P<.001) *Post hoc* tests indicate that there were significantly more cut stumps in the 10% residual (P=0.02) and 20%

residual (P=0.001) and significantly fewer logs in late stages of decay (Logs DC3) in the 20% residual (P<0.05) and 50% residual (P=0.02) treatments (Table 4-2).

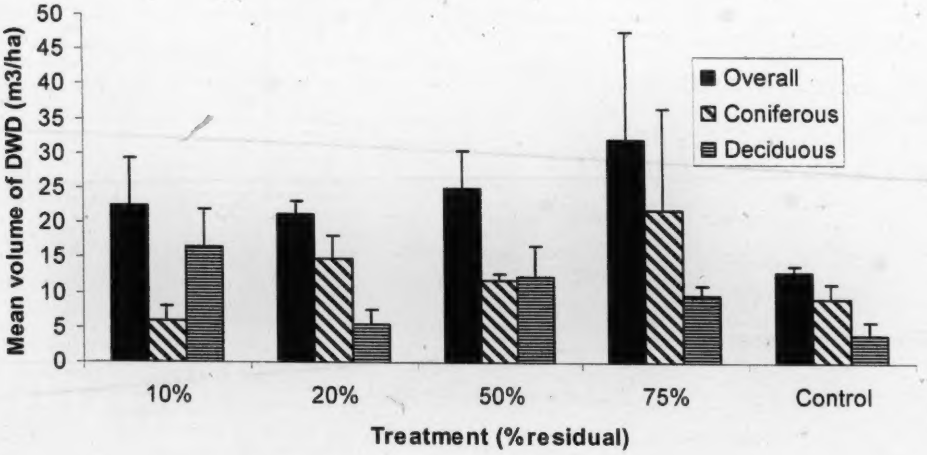

Figure 4-1 Mean ± 1 SE volume of downed woody debris (DWD) in each treatment.

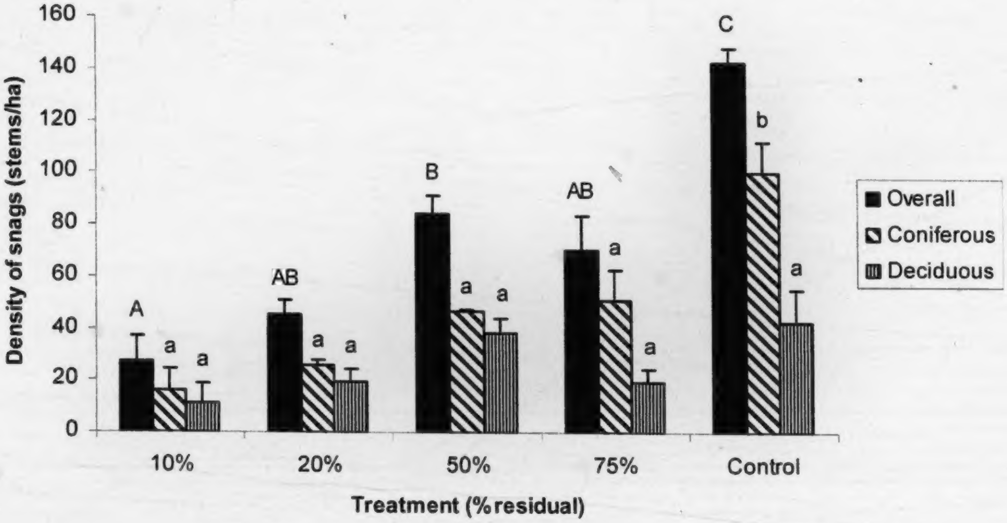

Figure 4-2 Mean ± 1 SE density of snags in each treatment. Capital letters denote overall treatment effects and lowercase letters denote results of Tukey's *post hoc* tests of differences within each treatment.

Table 4-2 Mean number of pieces of CWD in a 5m radius around each trap. Letters denote significant differences of CWD within each CWD category.

CWD Category	10% residual	20% residual	50% residual	75% residual	Controls
Natural Stumps	5.67 (a)	7.33 (a)	4.67 (a)	6.67 (a)	11.67 (a)
Cut stumps	16.67 (a)	20.00 (a)	8.33 (ab)	4.67 (ab)	0.00 (b)
Snags DC1	0.67 (a)	2.00 (a)	1.67 (a)	2.00 (a)	4.33 (a)
Snags DC2	2.67 (a)	1.33 (a)	5.00 (a)	2.67 (a)	5.67 (a)
Snags DC3	0.00 (a)	1.00 (a)	1.00 (a)	1.67 (a)	2.00 (a)
Logs DC1	8.33 (a)	8.67 (a)	13.33 (a)	12.00 (a)	15.33 (a)
Logs DC2	23.33 (a)	28.67 (a)	23.00 (a)	20.00 (a)	35.00 (a)
Logs DC3	17.67 (ab)	12.33 (a)	11.00 (a)	12.67 (ab)	28.00 (b)

Beetle species richness and abundance patterns. A total of 12,872 beetles were collected representing over 228 species. According to available life history information, 452 beetles representing 42 taxa were removed from the analysis as they were not saproxylic or could not be accurately separated to species (e.g. Aleocharinae). This resulted in a dataset of 12,420 saproxylic beetles representing 186 species. One hundred fifty one beetle species were collected on the girdled trees at an overall catch rate of 9 and 70 beetles per day in 2000 and 2001, respectively, and 148 species on naturally-killed trees at a rate of 21 and 11 beetles per day in 2000 and 2001, respectively. There were 38 species unique to girdled trees, 35 unique to naturally dead trees, and 113 species collected on both tree types. Grouping the species by their feeding ecology resulted in four feeding guilds: bark- and wood- borers, (8,965 individuals in 64 species); predators, (944 individuals in 53 species); fungivores (2418 individuals in 52 species), and scavengers (83 individuals in 13 species). Data concerning scavengers and beetles with an unknown functional group (7 individuals in 4 species) were not further analyzed separately because of the small sample sizes for these groups; however, data for these groups were included in analyses of overall saproxylic beetle species richness and ordination analyses.

Rarefaction estimates of overall saproxylic beetle assemblages grouped by harvesting treatment (Fig 4-3A), indicate that the controls collected the lowest abundance of beetles and species accumulated at a slightly faster rate in the 20% residual treatments than the other treatments. The 50% residual treatment accumulated species the slowest, followed by the controls, 75% residual, 10% residual, and the 20% residual treatment had the fastest accumulation rate of species. Although the curves have not flattened out, they are all past the inflection point indicating a majority of the species in these treatments were collected. The bark- and wood- feeding insects have the greatest separation between rarefaction curves indicating that the greatest differences of species richness occur in this feeding guild (Fig. 4-3B). The low retention treatments (10% and 20%) accumulate species the fastest and the 10% and 50% residual treatments collected the greatest number of beetles. There is little separation in the rarefaction curves between the treatments for the fungivores or predators (Fig.4-3C,D).

Significantly more saproxylic beetles were collected in 2001 compared to 2000 (ANOVA, $F_{1,20}$=10.46, P<0.01) (Fig 4-4A). Specifically there were significantly more wood- and bark- boring insects (ANOVA $F_{1,20}$=10.05, P<0.01) and fungivores (ANOVA, $F_{1,20}$=4.46, P<0.05) collected in 2001 compared to 2000 (Fig 4-4B,C). There were no significant harvesting treatment effects for all saproxylic beetles or any feeding group (Fig. 4-4).

Rarefaction estimates of species richness grouped by trap treatment for all saproxylic beetles indicate that the naturally dead trees accumulate species in all three feeding groups much faster than the trees killed by girdling (Fig 4-5). The biggest difference in species accumulation rates is exhibited by predators (Fig 4-5D) and the smallest by the fungivores (Fig 4-5C). For all feeding groups, although the rarefaction curves are still increasing, they are all past the inflection point indicating a majority of the species in these treatments were collected.

There was a significant effect of year (ANOVA, $F_{1,56}$=10.30, P<0.01) and trap treatment (ANOVA, $F_{1,56}$=9.09, P<0.01) on catch of all saproxylic beetle species (Fig 4-6A). The interaction between year and trap treatment was also significant (ANOVA, $F_{1,56}$=19.69, P<0.001). Tukey's tests show that there were significantly more beetles collected on girdled trees in 2001 than on either girdled trees in 2000 (P<0.001), naturally dead trees in 2000 (P<0.001) and naturally dead trees in 2001 (P<0.001). The same pattern exists in the wood- or bark- borers (Fig 4-6B). Similar patterns are seen with the fungivores (Fig 4-6C) and predators (Fig 4-6D) although the differences are not as great.

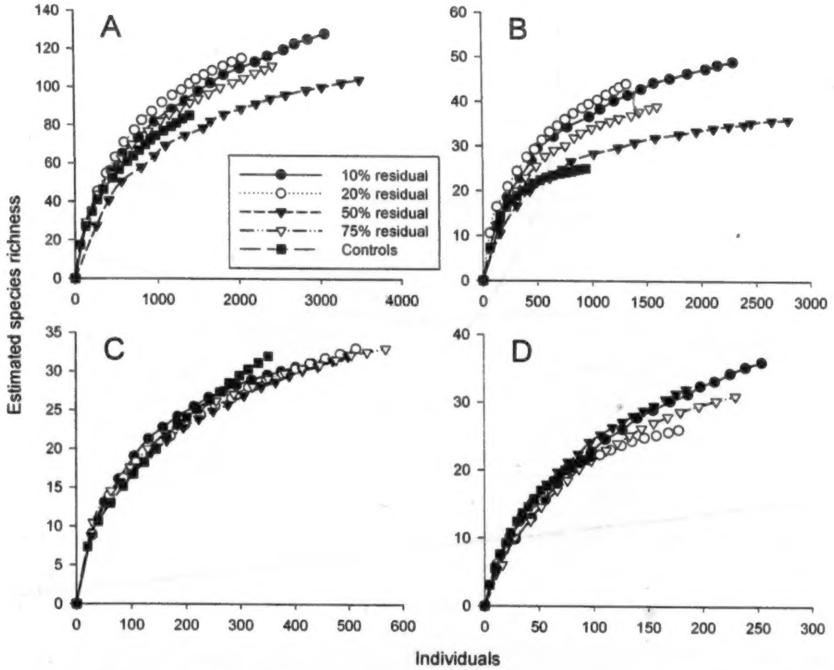

Figure 4-3 Rarefaction curves for: A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores, and D) predators for all harvesting treatments.

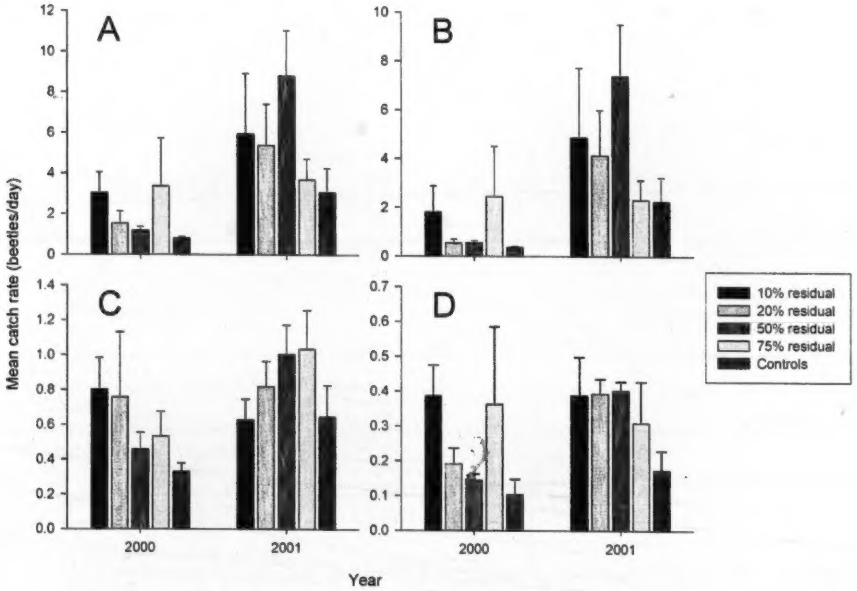

Figure 4-4 Mean standardized catch of: A) all saproxylic beetles; B) bark- and wood-borers; C) fungivores, and D) predators for all harvesting treatments grouped by year. Error bars represent 1 SE above the mean.

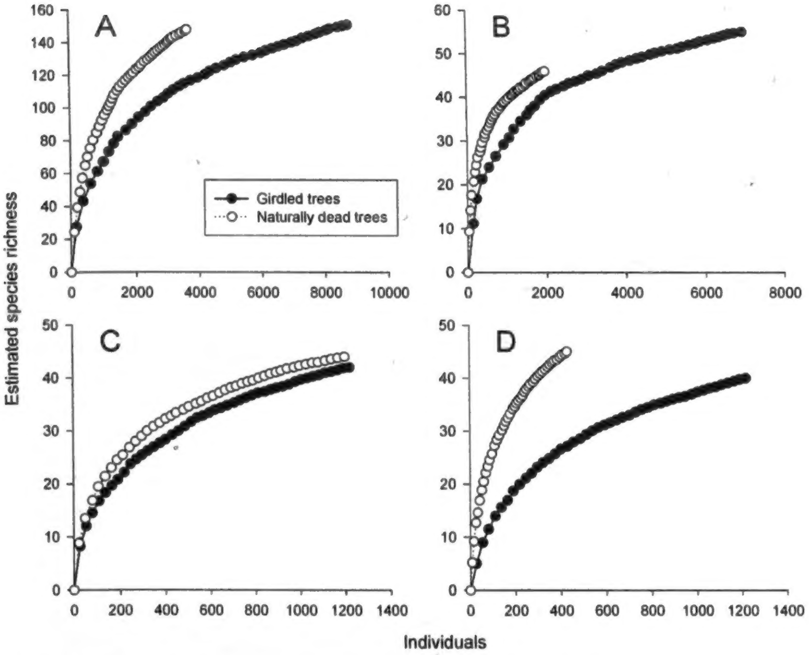

Figure 4-5 Rarefaction curves for: A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores, and D) predators collected from trees killed by girdling and naturally dead trees.

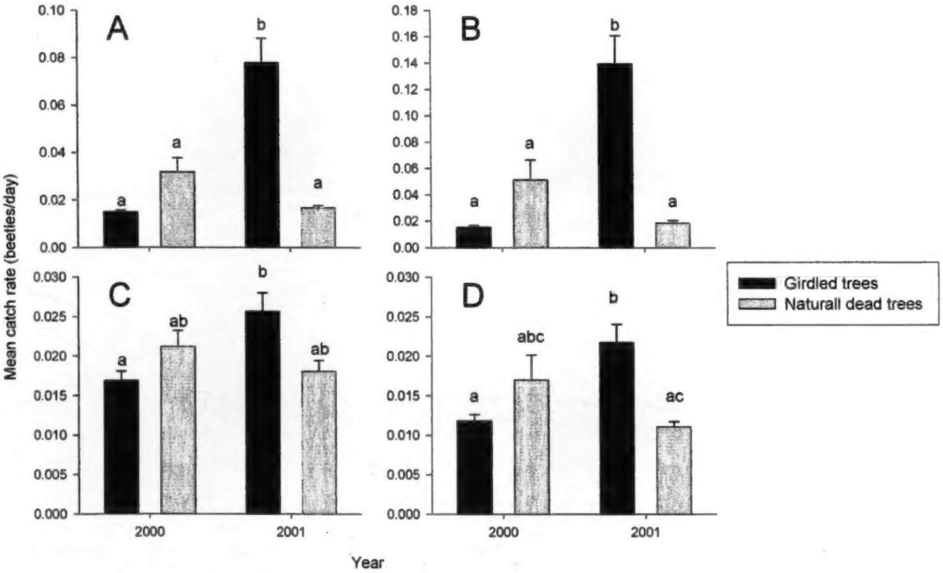

Figure 4-6 Mean catch rate of A) all saproxylic beetles; B) bark- and wood- borers; C) fungivores, and D) predators, collected from trees killed by girdling and naturally dead trees. Error bars represent 1 SE above the mean.

Assemblage composition. Difference in beetle assemblage composition was analyzed using NMS ordination and indicator analysis. Ordination of all beetles was unsuccessful as there was too much variation in the data to produce a significant ordination. Similar problems were encountered when grouping the years together due to temporal variability. Ordination of each year independently for each feeding guild provided the most significant results.

NMS ordinations of wood- and bark-borers in 2000 (Fig. 4-7A,B) resulted in a 2-dimensional solution with a stress of 15.8, which was significantly different from randomized data (Monte Carlo, $P<0.02$). When coded by harvesting treatment, the ordination shows a distinct group of 5 of the 6 control stands in the bottom right quadrant (Fig. 4-7A). There is little separation among the remaining sample points. The ordination coded by type of trap treatment showed no separation in overall beetle assemblage structure between trees that were girdled or that died naturally in 2000, although natural snags exhibited more variability than did girdled snags (Fig. 4-7B).

NMS ordination of wood- and bark- borers in 2001 (Fig. 4-7C,D) resulted in a 2-dimensional solution with a stress of 12.4. The ordination coded by harvesting treatment (Fig. 4-7C) has no apparent groupings based on harvesting intensity, suggesting that beetle assemblage heterogeneity is not particularly related to the experimental treatments. Surprisingly, even the control stands did not group closely together. The ordination coded by trap treatment shows clear groupings of beetle assemblages on girdled and naturally dead trees, indicating that the beetle assemblages did respond more to trap treatment (CWD quality) than to harvesting treatment 2.5 years after harvesting.

Ordination of fungivores in 2000 did not produce any significant solutions. This is probably because two traps, one each from naturally dead trees in the 10% and 20% residual treatments, collected over twice as many beetles as did all other traps. These two large catches reflected high abundances of two fungivorous species, *Xylita laevigata* (Hellenius) and *Molamba obesa* Casey, that constituted *c.* 70% of the catch in both traps. After these two samples were removed, NMS ordination resulted in a significant 2-dimensional solution with stress of 19.8 (Monte Carlo, $P=0.04$) (Fig. 4-8A,B). The only pattern apparent in the ordination when coded by harvesting treatment (Fig 4-8A) was that the control samples grouped together to the right of axis 2; while the remaining treatments were widely dispersed. Coding the ordination by trap treatment (Fig. 4-8B), the girdled trees appear to cluster along axis 1, whereas the naturally dead trees are more scattered around axis 2.

Ordination of fungivores in 2001 resulted in a significant 2-dimensional solution with a stress of 20.7 ($P=0.04$, Monte Carlo test) (Fig. 4-8C,D). Coding the ordination by harvesting treatment (Fig. 4-8C) reveals a weak treatment effect along axis 1, which explains 29% of the variance, with the control plots on the left and the low retention treatments on the right. Axis 2 is more significant, explaining 43% of the variance, and provides a clear separation between trap treatments (Fig. 4-8D).

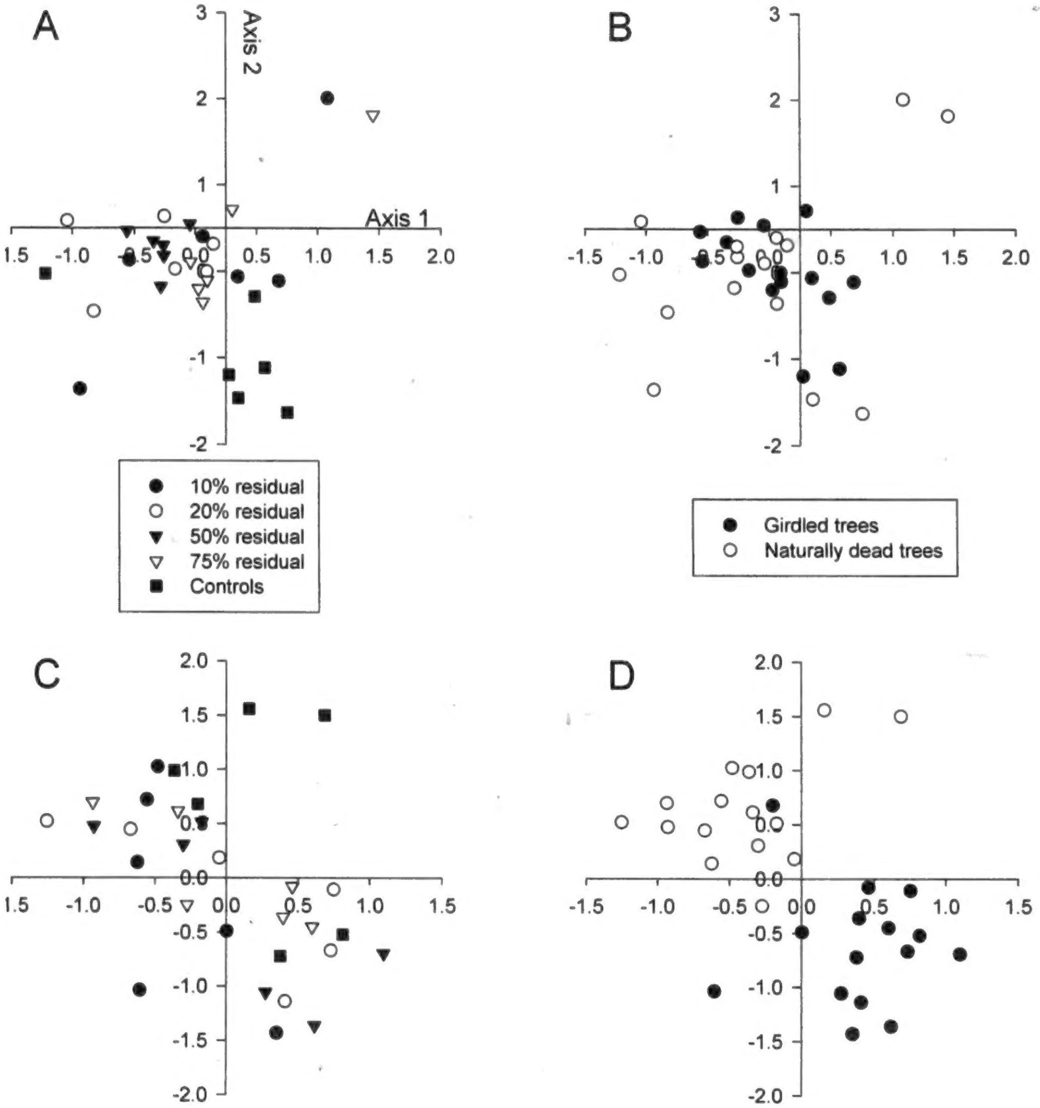

Figure 4-7 NMS ordination of wood- and bark- boring beetles: A) year 2000 grouped by harvesting treatment; B) year 2000 grouped by trap treatment; C) year 2001 grouped by harvesting treatment, and D) year 2001 grouped by trap treatment.

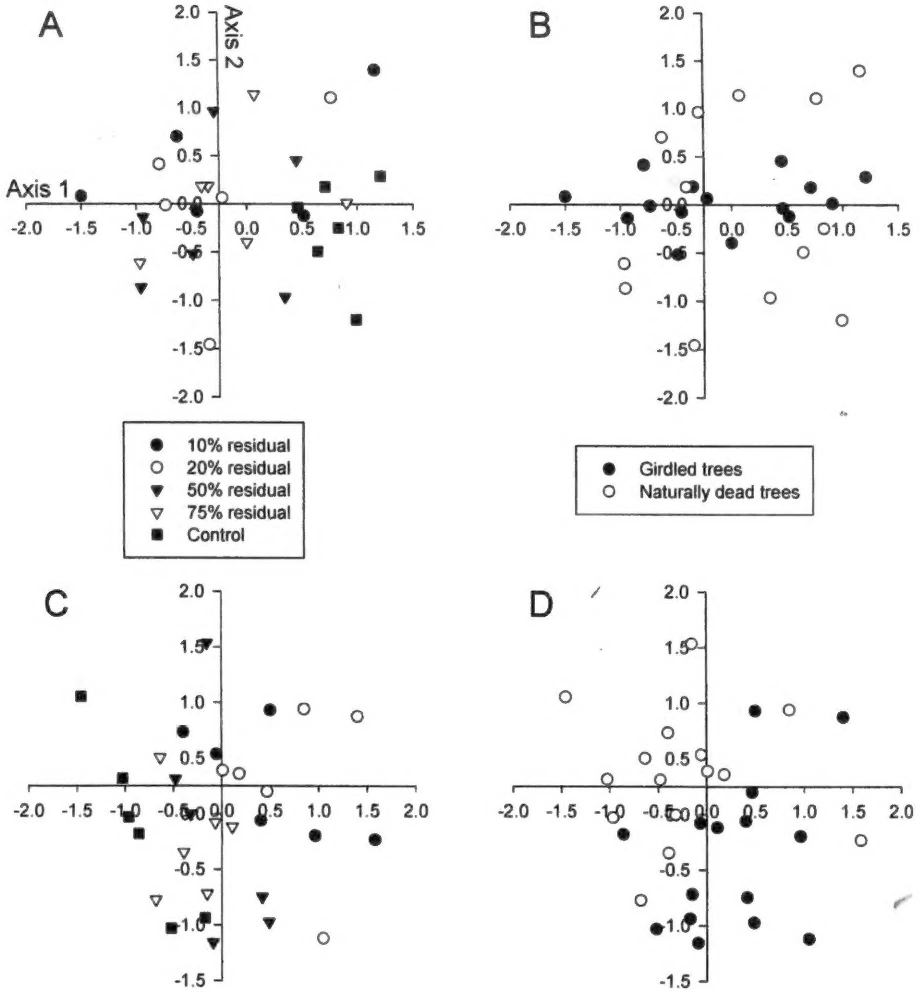

Figure 4-8 NMS ordination of fungivores: A) year 2000 grouped by harvesting treatment; B) 2000 grouped by trap treatment; C) year 2001 grouped by harvesting treatment, and D) year 2001 grouped by trap treatment.

Ordination of predators in 2000 did not produce any significant solutions for predatory beetles because two samples from control stands were significant outliers (the mean distance of these samples fell greater than 2 standard deviations from the mean Bray-Curtis distance between all samples) because both traps collected very few species and individuals. With these two samples removed from the analysis, a significant 2-dimensional ordination solution was found with a stress of 21.0 (P=0.04) (Fig. 4-9A,B). Coding the ordination by harvesting treatment reveals little pattern except that the control treatments appear to group loosely in the bottom left with a slight trend of decreasing retention moving towards the top right of the ordination (Fig. 4-9A). Coding year 2000 catches of predatory beetles by tree type revealed no patterns (Fig. 4-9B).

Ordination of predatory beetles in 2001 has a significant 2-dimensional solution with a stress of 17.6 (P=0.02, Monte Carlo test) (Fig. 4-9C,D). Although there was no apparent pattern in relation to harvesting treatment (Fig. 4-9C), there was a clear separation of predatory beetle assemblages between girdled trees and naturally dead trees (Fig. 4-9D). Furthermore, the ordination reveals a lot more variation of sample points for the traps on naturally dead trees than in those on the girdled trees.

The minor nature of harvesting treatment effects on saproxylic beetles is further supported by species indicator analysis that found only 9 species to be significant indicators of harvesting treatment, 6 in 2000 and 3 in 2001 (Table 4-3). No species were consistent indicators for both years. Species indicator analysis of trap tree type revealed 19 species to be significant indicators, 16 in 2001, and no species were consistent indicator for both years (Table 4-3). Furthermore, 6 of the significant indicators were fungivorous, 11 were bark- and wood-boring beetles, and 2 were predators. All the bark- and wood-boring species, the two predators (both closely associated with bark beetles), and the *Epuraea linearis* Mäklin (characteristically inhabiting trees recently colonized by bark beetles), were all indicative of the girdled trees.

Multivariate regression analysis consistently produced a two leafed tree. The single split in the tree was between girdled and naturally dead trees, explaining 29% of the variance in the data (CV error= 0.806, SE= 0.132). Harvesting intensity and CWD quantity were not related to the saproxylic beetle assemblages. This further supports the trend that the biggest determining factor of saproxylic beetle assemblages in conifer dominated stands is the quality (time since death) of CWD.

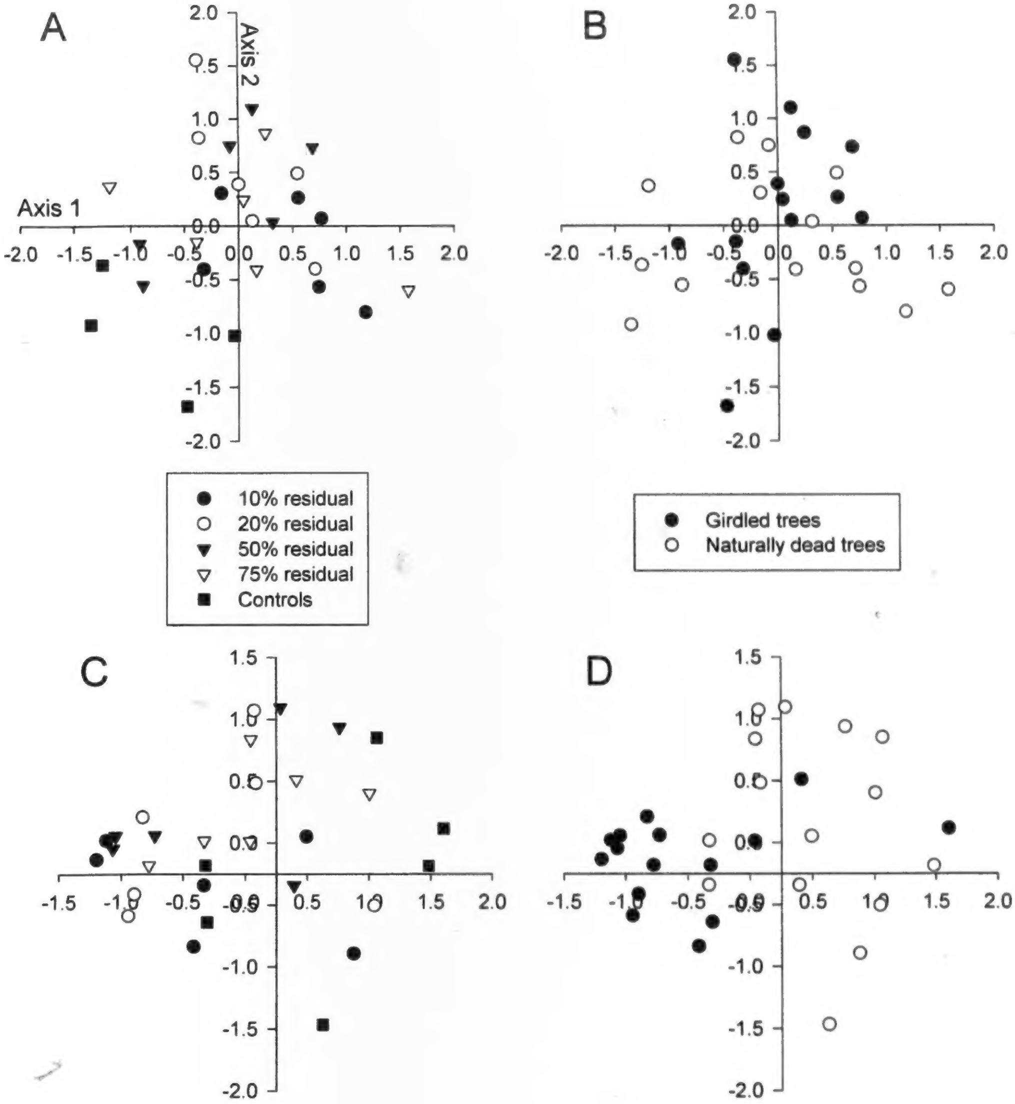

Figure 4-9 NMS ordination of predators: A) year 2000 grouped by harvesting treatment; B) year 2000 grouped by trap treatment; C) year 2001 grouped by harvesting treatment, and D) year 2001 grouped by trap treatment.

Table 4-3 Significant indicator species of harvesting and trap treatments.

Functional group	Year	Family	Species	Treatment (harvest or trap)	Observed indicator value	Indicator value from randomized tests	
						Mean±SD	P value
Fungivore	2000	Lathridiidae	*Enicmus tenuicornis* LeConte	75% Residual	38.3	16.1±9.5	0.038
Fungivore	2000	Erotylidae	*Triplax californica* LeConte	10% Residual	38.2	16±9.07	0.042
Fungivore	2001	Cryptophagidae	*Cryptophagus tuberculosus* Maklin	Control	63.1	21.5±8.9	0.002
Fungivore	2001	Lathridiidae	*Melanophthalma villosa* (Zimmermann)	75% Residual	33.3	26±3.34	0.023
Tree Feeder	2000	Scolytidae	*Xylechinus montanus* Blackman	Control	47.6	21.5±8.09	0.01
Tree Feeder	2000	Scolytidae	*Pityophthorus* spp.	75% Residual	47.5	21.7±9.49	0.019
Tree Feeder	2000	Scolytidae	*Scolytus piceae* (Swaine)	10% Residual	41.7	16.6±8.93	0.045
Predator	2000	Cucujidae	*Pediacus fuscus* Erichson	10% Residual	57.5	27.3±11.29	0.018
Predator	2001	Staphylinidae	*Quedius velox* Smetana	75% Residual	35.8	19.8±7.92	0.033
Fungivore	2000	Melandryidae	*Xylita livida* (C.R.Sahlberg)	Natural	48.6	25±6.99	0.008
Fungivore	2000	Leiodidae	*Anisotoma* sp. (pb. *globososa* Hatch)	Natural	33.3	15.4±5.72	0.035
Predator	2001	Colydiidae	*Lasconotus complex* LeConte	Girdled	78.4	32.8±8.94	0.001
Fungivore	2001	Nitidulidae	*Epuraea linearis* Mäklin	Girdled	75.7	50.3±6.98	0.005
Fungivore	2001	Melandryidae	*Serropalpus substriatus* (Haldeman)	Girdled	43.9	26.5±8.45	0.018
Fungivore	2001	Melandryidae	*Xylita laevigata* (Hellenius)	Natural	52.3	31.1±8.57	0.02
Fungivore	2001	Corylophidae	*Molamba obesa* Casey	Girdled	69.2	53.6±8.51	0.046
Tree Feeder	2000	Curculionidae	*Pissodes rotundatus* LeConte	Girdled	52	26.8±7.65	0.008
Tree Feeder	2001	Scolytidae	*Polygraphus rufipennis* (Kirby)	Girdled	97.3	53.1±8.02	0.001
Tree Feeder	2001	Scolytidae	*Dendroctonus rufipennis* (Kirby)	Girdled	86.4	51.3±9.94	0.001
Tree Feeder	2001	Scolytidae	*Scolytus piceae* (Swaine)	Girdled	77.4	33.7±8.33	0.001
Tree Feeder	2001	Cerambycidae	*Spondylis upiformis* Mannerheim	Girdled	66.7	25.5±7.44	0.001
Tree Feeder	2001	Scolytidae	*Dryocoetes affaber* (Mannerheim)	Girdled	91.4	57.1±10.14	0.002

Functional group	Year	Family	Species	Treatment (harvest or trap)	Observed indicator value	Indicator value from randomized tests	
						Mean±SD	P value
Tree Feeder	2001	Scolytidae	*Cryphalus ruficollis ruficollis* Hopkins	Girdled	67.4	42.7±8.96	0.007
Tree Feeder	2001	Scolytidae	*Trypodendron lineatum* (Olivier)	Girdled	83.2	54.4±10.83	0.01
Tree Feeder	2001	Scolytidae	*Scierus annectans* LeConte	Girdled	70.4	46.6±9.32	0.012
Tree Feeder	2001	Scolytidae	*Crypturgus borealis* Swaine	Girdled	84.1	56±12.18	0.015
Tree Feeder	2001	Cerambycidae	*Tetropium parvulum* Casey	Girdled	40	17.2±6.35	0.019
Predator	2001	Cleridae	*Thanasimus undatulus* (Say)	Girdled	83.6	44.9±6.9	0.001

Discussion

Saproxylic beetles did not respond differentially to harvesting treatments in the second or third summers post-harvest. However, all three feeding groups studied appear to respond strongly to trap treatment (newly girdled trees versus trees naturally killed 5-8 years previously). Variation in quality (time since death) of CWD appears to be the most important factor determining saproxylic beetle assemblages at the EMEND site. There were few differences in the stand-level volumes and local-level quantity of CWD across the treatments, with the notable exception that increased harvest intensity had an adverse effect on the density of snags. However, over the long term, as stands age, those with higher retention will undoubtedly experience greater input of CWD, and subsequent benefits of VR for conservation of saproxylic beetles are likely to become more evident.

Based on a wide range of North European studies, Siitonen (2001) stated that the main factors determining species composition in a dead trunk are tree species, stage of decay, and species of fungi decaying the trunk. Furthermore, the amount of CWD in an area will also affect saproxylic beetle assemblages through increases to local species populations, greater diversity of CWD quality and by increasing probability of colonization from neighboring CWD (Siitonen 2001).

Variable retention (VR) harvesting

There was no observed effect of harvesting treatment on assemblage structure of bark- and wood-feeding or predatory beetles. Fungivores, in contrast, were slightly affected in 2000 and more profoundly affected in 2001, possibly reflecting changes in fungus flora colonizing CWD. As stands are increasingly opened, it is anticipated that the increased sunlight and heat will result in drier CWD than in more shaded stands, thereby possibly adversely affecting some fungal species and the arthropods feeding on them. This hypothesis is supported by the fact that three fungus feeding species, *Enicmus tenuicornis, Cryptophagus tuberculosus* and *Melanophthalma villosa*, were indicative of high retention treatments (control or 75% residual). These small cryptic species are all thought to feed on molds in decaying organic matter (Woodroffe and Coombs 1961, White 1983). Fungivores were the only group which demonstrated early effects of VR harvesting, possibly indicating that they are more sensitive than other groups and, therefore, should be of particular focus for conservation efforts.

There is a similar trend in the bark- and wood-feeding beetle as the two species indicative of high retention are small cryptic taxa (*Xylechinus montanus* and *Pityophthorus* spp.). Little is known about the biology of these species; *X. montanus* is thought to attack small, weakened, usually suppressed spruce trees and *Pityophthorus* spp. are generally found in twigs and small branches (Bright 1976). Neither of these beetles had a preference for small trees in this study. These small beetles are probably more susceptible to changes in the microclimate of the trees due to forest harvest. As harvesting opens up the stands, snags likely experience increased surface and sub-surface temperatures. Interestingly, Peltonen and Heliövaara (1998) found that

Xylechinus pilosus (Ratzeburg) was a forest interior species in Finland. It may be that members of this genus of bark beetles are useful indicators of undisturbed forest interiors.

Similarity of beetle assemblages, especially tree-feeding and predatory beetles, across treatments likely reflects the lack of change in CWD quantity across the treatments. It is well known that the main factor determining saproxylic beetle assemblages is CWD quality and quantity (Siitonen 2001), therefore without changes in the CWD after harvesting there is little immediate impact on saproxylic beetle assemblages. As these stands age, the differences in CWD in the different harvesting treatments will become more evident as trees dies and should result in altered saproxylic beetle assemblages. It is also possible that it is still too soon after the disturbance to observe any major changes in the saproxylic beetle assemblages. Beetles may still be persisting from the pre-disturbance forest in addition to the open habitat specialists colonizing the newly harvested areas. This phenomenon has also been observed in carabids (Niemelä et al. 1988, Niemelä et al. 1993).

Course woody debris quality

The changes in saproxylic beetle assemblages on girdled and naturally dead trees are clear responses to variation in CWD quality (time since death). The girdled trees represent mortality that is much earlier in the decay process than the naturally dead trees. Thus, beetles feeding predominately on live or recently dead phloem tissue were attracted to the girdled snags, but snags that were naturally dead had passed through the stages preferred by these early successional species. Additionally some fungivore, scavenger or predatory species require preconditioning of trees by bark beetles and other wood- and bark- boring species (Hammond et al. 2001), and these species may not have been able to successfully colonize the girdled trees until at least the second year of study or not at all.

Data about species composition show that girdled trees were in the initial successional stage of decay in 2001, and according to the species indicator analysis, 10 species of scolytid and cerambycid beetles were associated with these trees. Many of these beetle species were also present in 2000, but low numbers (9 beetles per day) may have prevented strong associations from being recognized. Catch was much higher in 2001 (70 beetles per day), perhaps because several species were collected in 2000 while attacking the tree and in 2001 beetles were collected both attacking the tree and emerging from the tree after successful reproduction. This idea is further supported by the large numbers (*c.* 40%) of teneral or light colored beetles, especially *Trypodendron lineatum* and *Polygraphus rufipennis*, observed during identification. *P. rufipennis*, the strongest indicator of girdled trees (97.3) emerges in late May or early June when they overwinter as adults, or in late June or July when they overwinter as larvae or pupae (Bright 1976). The peak in abundance of *P. rufipennis* in this study for both years was in late June, indicating that pupae or larvae overwintered.

The faunal similarity between dead and girdled trees in 2000 could reflect an equal chance of visitation of naturally killed or girdled snags, both of which produce ethanol, an attractant for many bark- and wood-boring species. However, as only girdled trees were acceptable for feeding and reproduction by many of these species, due to the requirement for fresh phloem for most species, only girdled trees yielded large numbers of these species in 2001, resulting in significant differences in assemblage structure among the two groups of trees in 2001.

As only a sub-set of the total variety of spruce CWD was sampled in this study (*i.e.*, snags dead for 1-2 years and 5-8 years), only a part of the saproxylic beetle community was sampled. Sampling of snags of additional decay classes, logs, and woody debris of the full range of sizes, as well as collecting from identifiable micro-habitats (*e.g.*, conks, hollows, branch tips), would undoubtedly result in many more species. There remains the question of whether fauna associated with other CWD qualitative categories may have fauna that is more sensitive to harvesting immediately after treatment. In this study, examination of the full range of CWD was prohibited by shortage of resources.

Management Implications

Although harvesting had little immediate effect on most species of saproxylic beetles in the coniferous cover type at EMEND, dependence of this community on dead and decaying wood will likely become evident as the input of dead and decaying wood is altered so that successional classes of decaying CWD are eliminated or pushed to great rareness. The greater the proportion of trees taken from the forest during the first harvest, the greater the decrease in the amount of CWD input in the future. Also, it is possible that the reduced availability of trees for CWD recruitment will also result in reduced qualitative variability of CWD, and reduction or loss of micro-habitat types and associated fauna and flora. It is this large scale reduction of CWD quantity and quality that is the greatest threat to saproxylic beetle communities.

The benefits of variable retention harvesting on saproxylic beetles cannot be fully evaluated at this time. Therefore, considering only short term impacts, there are no immediate benefits for the conservation of this group of beetles realized by only partially cutting the forest. Ultimately benefits of VR will depend on cutting a smaller portion of many stands having advantages over cutting a large proportion of fewer stands. Benefits of VR for saproxylic beetles are anticipated to become more evident at EMEND as these stands age, and the amount (and possibly quality) of CWD within each treatment begins to diverge more significantly. Although we have clear evidence that there are lower limits to volume of CWD required to support a rich saproxylic fauna (Siitonen & Martikainen 1994), the implications of variation in CWD produced across landscapes by forestry activities remain to be thoroughly studied.

Literature Cited

Alexander, K. N. A. 1995. Historic parks and pasture-woodlands: The National Trust resource and its conservation. Biological Journal of the Linnean Society **56**:155-175.

Arnett, R. H. J., and M. C. Thomas. 2001a. American beetles v. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, Florida.

Arnett, R. H. J., and M. C. Thomas. 2001b. American beetles v. 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, Florida.

Bousquet, Y. 1991. Checklist of beetles of Canada and Alaska. Agriculture Canada, Ottawa, Ont.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. G. Stone. 1984. Classification and regression trees. Wadsworth International Group, Belmont, California, USA.

Bright, D. E. J. 1976. The insects and arachnids of Canada and Alaska. Part 2. The bark beetles of Canada and Alaska (Coleoptera: Scolytidae). Canada Department of Agriculture, Ottawa, Canada.

Bunnell, F. L., L. L. Kremsater, and E. Wind. 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands. Environmental Reviews **7**:97-146.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Clayquot Scientific Panel. 1995. Scientific panel for sustainable forest practices in Clayquot Sound, Report 5, Sustainable ecosystem management in Clayquot Sound: planning and practices. Victoria, B.C.

Colwell, R. K. 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

De'Ath, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. Ecology **83**:1105-1117.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Franklin, J. F., D. A. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Island Press, Washington, D.C.

Hammond, H. E., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research **31**:1175-1183.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. Canadian Entomologist **129**:1009-1033.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research **34**:1-19.

Käila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica **29**:21-23.

Magurran, A. E. 1988. Ecological diversity and its measurment. Princeton University Press, Princeton, New Jersey.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletin **49**:205-218.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation **94**:199-209.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, OR.

McCune, B., and M. J. Medford. 1999. PCOrd software: multivariate analysis of ecological data. MJM Software. Gleneden Beach, OR.

McGill, W. E., and J. R. Spence. 1985. Soil fauna and soil structure: feedback between size and architecture. Quaestiones Entomologicae **21**:645-654.

Niemelä, J., Y. Haila, E. Halme, T. Lajti, T. Pajunen, and P. Punttila. 1988. The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forests. Annales Zoologici Fennici **25**:107-119.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clearcut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology **7**:551-561.

Peltonen, M., and K. Heliövaara. 1998. Incidence of Xylechinus pilosus and Cryphalus saltuarius (Scolytidae) in forest-clearcut edges. Forest Ecology and Management **103**:141-147.

R. Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.

Reichle, D. E. 1977. The role of soil invertebrates in nutrient cycling. Ecological Bulletins **25**:145-156.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins **49**:11-41.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russion Karelia. Scandinavian Journal of Forest Research **9**:185-191.

Simila, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation **106**:19-27.

Sippola, A. L., J. Siitonen, and P. Punttila. 2002. Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. Annales Zoologici Fennici **39**:69-86.

Van Wagner, C. E. 1968. The line intersect method for forest fuel sampling. Forest Science **14**:20-26.

White, R. E. 1983. A Field Guide to the Beetles: of North America. Houghton Mifflin, Boston.

Woodroffe, G. E., and C. W. Coombs. 1961. A revision of the North American *Cryptophagus* Herbst (Coleoptera: Cryptophagidae). Miscellaneous Publications of the Entomological Society of America **2**:179-211.

Work, T. T., D. P. Shorthouse, J. R. Spence, W. J. A. Volney, and D. W. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research **34**:417-430.

Appendix 4-A

Saproxylic beetles collected from flight intercept traps on dead and girdled trees from coniferous dominated stands with variable levels of tree retention.

Family	Species	Feeding group	Harvesting treatment	Trap treatment
Anobiidae	*Ernobius* sp.	Wood- and bark- borer	10	Girdled
	Xestobium sp.	Wood- and bark- borer	75	Dead
	Hemicoelus carinatus (Say)	Wood- and bark- borer	10, 20, 50, 100	Girdled, Dead
	Microbregma emarginatum emarginatum (Duftschmid)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Ptilinus lobatus Casey	Wood- and bark- borer	10	Dead
	Utobium elegans (Horn)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
Buprestidae	*Agrilus liragus* Barter & W.J.Brown	Wood- and bark- borer	10, 20	Girdled, Dead
	Anthaxia inornata (Randall)	Wood- and bark- borer	10, 20, 50	Dead
	Chrysobothris trinervia (Kirby)	Wood- and bark- borer	10	Dead
	Dicerca tenebrica (Kirby)	Wood- and bark- borer	10, 20	Girdled, Dead
	Dicerca tenebrosa (Kirby)	Wood- and bark- borer	10, 20	Girdled, Dead
	Melanophila fulvoguttata (Harris)	Wood- and bark- borer	10	Girdled, Dead
Cantharidae	*Dichelotarsus piniphilus* (Eschscholtz)	Predator	10, 20, 50, 75, 100	Girdled, Dead
Carabidae	*Agonum retractum* LeConte	Predator	75, 100	Girdled
	Bembidion grapii Gyllenhal	Predator	10	Girdled
	Bembidion timidum (LeConte)	Predator	20	Dead
	Bradycellus lecontei Csiki	Predator	10	Dead
	Calathus advena (LeConte)	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Dicheirotrichus cognatus (Gyllenhal)	Predator	10, 20	Girdled, Dead
	Platynus decentis (Say)	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Pterostichus adstrictus Eschscholtz	Predator	10, 20, 50, 75	Girdled, Dead
	Sericoda quadripunctata (DeGeer)	Predator	100	Dead
	Stereocerus haematopus (Dejean)	Predator	10, 20, 50	Girdled, Dead

Family	Species	Feeding group	Harvesting treatment	Trap treatment
Cephaloidae	*Cephaloon tenuicorne* LeConte	Wood- and bark- borer	10, 20, 50, 75	Girdled, Dead
Cerambycidae	*Acmaeops proteus proteus* (Kirby)	Wood- and bark- borer	10, 20, 50, 75	Girdled, Dead
	Arhopalus foveicollis (Haldeman)	Wood- and bark- borer	10, 50	Girdled
	Asemum striatum (Linné)	Wood- and bark- borer	20, 50, 75	Girdled
	Meriellum proteus (Kirby)	Wood- and bark- borer	20, 75, 100	Girdled
	Monochamus scutellatus scutellatus (Say)	Wood- and bark- borer	10, 20	Girdled
	Neacanthocinus pusillus (Kirby)	Wood- and bark- borer	10, 20, 50	Girdled
	Neoclytus muricatulus muricatulus (Kirby)	Wood- and bark- borer	10	Girdled
	Pachyta lamed liturata Kirby	Wood- and bark- borer	10, 20	Girdled
	Phymatodes dimidiatus (Kirby)	Wood- and bark- borer	10, 50, 75, 100	Girdled, Dead
	Pogonocherus penicillatus LeConte	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Rhagium inquisitor (Linné)	Wood- and bark- borer	10, 20, 75	Girdled, Dead
	Spondylis upiformis Mannerheim	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Tetropium parvulum Casey	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Tetropium sp.	Wood- and bark- borer	10, 75, 100	Girdled
	Xylotrechus undulatus (Say)	Wood- and bark- borer	10, 20, 50, 75	Girdled, Dead
Cerylonidae	*Cerylon castaneum* Say	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
Ciidae	*Cis fuscipes* Mellié	Fungivore	10, 50, 75, 100	Girdled, Dead
	Cis sp.	Fungivore	10, 20, 50	Girdled, Dead
	Dolichocis manitoba Dury	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Hadraule blaisdelli (Casey)	Fungivore	100	Girdled
	Octotemnus laevis Casey	Fungivore	100	Dead
	Sulcacis curtula (Casey)	Fungivore	50, 75	Girdled
Clambidae	*Clambus pubescens* Redtenbacher	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
Cleridae	*Thanasimus undatulus nubilus* (Say)	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Thanasimus undatulus undulatus (Say)	Predator	10, 20, 50, 75, 100	Girdled, Dead
Colydiidae	*Lasconotus* complex LeConte	predator	20	Girdled
Corylophidae	*Molamba obesa* Casey	Fungivore	10, 20, 50, 75, 100	Girdled, Dead

Family	Species	Feeding group	Harvesting treatment	Trap treatment
Cryptophagidae	*Antherophagus ochraceus* Melsheimer	Fungivore	100	Girdled
	Atomaria sp.	Fungivore	20, 75, 100	Girdled, Dead
	Caenoscelis antennalis (Casey)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Cartodere constricta (Gyllenhal)	Fungivore	10	Girdled
	Cryptophagus tuberculosus Maklin	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Cryptophagus varus Woodroffe & Coombs	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Ephistemus globulus (Paykull)	Fungivore	100	Dead
	Henoticus serratus (Gyllenhal)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
Cucujidae	*Cucujus clavipes puniceus* Mannerheim	Predator	10, 50	Girdled, Dead
	Dendrophagus cygnaei Mannerheim	Predator	10, 20, 50	Girdled, Dead
	Pediacus fuscus Erichson	Predator	10, 20, 50, 75	Girdled, Dead
Curculionidae	*Pissodes rotundatus* LeConte	Wood- and bark- borer	50	Girdled
	Cossonus pacificus Van Dyke	Wood- and bark- borer	20, 75	Girdled, Dead
	Hylobius pinicola (Couper)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Magdalis subtincta LeConte	Wood- and bark- borer	10, 20, 75	Girdled, Dead
	Rhyncolus brunneus Mannerheim	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Scaphomorphus sp.	Wood- and bark- borer	50	Girdled
Dermestidae	*Dermestes lardarius* Linné	Scavenger	75	Girdled
Elateridae	*Ampedus apicatus* (Say)	Predator	10	Girdled, Dead
	Ampedus deletus (LeConte)	Scavenger	10, 20, 75, 100	Girdled, Dead
	Ampedus luctuosus (LeConte)	Scavenger	10	Girdled
	Ampedus miniipennis (LeConte)	Scavenger	20, 50, 100	Girdled, Dead
	Ampedus nigrinus (Herbst)	Unknown	10, 100	Girdled
	Ctenicera resplendens (Eschs.)	Scavenger	10, 20, 75	Girdled, Dead
	Denticollis denticornis (Kirby)	Scavenger	20, 75	Girdled, Dead
Erotylidae	*Triplax californica* LeConte	Fungivore	10, 50	Girdled, Dead
	Triplax flavicollis Lacordaire	Fungivore	20	Girdled
Eucinetidae	*Epiphanis cornutus* Eschscholtz	Fungivore	100	Dead

Family	Species	Feeding group	Harvesting treatment	Trap treatment
	Eucinetus punctulatus LeConte	Fungivore	10, 100	Girdled, Dead
Histeridae	*Hister* sp.	Predator	10, 50, 75, 100	Girdled, Dead
	Hololepta aequalis Say	Predator	20	Girdled
	Platysoma lecontei Marseul	Predator	10, 20, 75	Girdled, Dead
Hydrophilidae	*Cercyon herceus frigidus* Smetana	Predator	10	Dead
Lathridiidae	*Cartodere constricta* (Gyllenhal)	Fungivore	10, 20, 50, 75	Girdled, Dead
	Corticaria serrata (Paykull)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Corticaria sp.	Fungivore	10, 20, 50, 75	Girdled, Dead
	Enicmus mimus Fall	Fungivore	10, 75	Girdled, Dead
	Enicmus tenuicornis LeConte	Fungivore	50, 75, 100	Girdled, Dead
	Lathridius hirtus Gyllenhal	Fungivore	20, 75	Girdled, Dead
	Lathridius minutus (Linné)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Melanophthalma villosa (Zimmermann)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
Leiodidae	*Agathidium* sp.	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Anistoma sp.	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
Lycidae	*Dictyopterus aurora* (Herbst)	Fungivore	100	Girdled
	Dictyopterus thoracicus (Randall)	Fungivore	75	Dead
Lymexylidae	*Hylecoetus lugubris* Say(+)	Wood- and bark- borer	75	Dead
Melandryidae	*Dryocoetes autographus* (Ratzeburg)	Wood- and bark- borer	20	Dead
	Enchodes sericea (Haldeman)	Scavenger	10, 20, 50	Girdled
	Melandrya striata Say	Scavenger	10, 20, 50, 75	Girdled, Dead
	Serropalpus substriatus Haldeman	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Xylita laevigata (Hellenius)	Fungivore	10, 20, 50, 75	Girdled, Dead
	Xylita livida (C.R.Sahlberg)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Zilora hispida LeConte	Scavenger	10	Dead
Mycetophagidae	*Mycetophagus quadriguttatus* P.W.J.Muller	Fungivore	20, 75	Girdled, Dead
	Mycetophagus distinctus Hatch	Fungivore	10, 100	Girdled, Dead
Nitidulidae	*Epuraea linearis* Mäklin	Fungivore	10, 20, 50, 75, 100	Girdled, Dead

Family	Species	Feeding group	Harvesting treatment	Trap treatment
	Glischrochilus moratus W.J.Brown	Fungivore	10, 20, 50	Girdled, Dead
	Glischrochilus sanguinolentus sanguinolentus (Olivier)	Predator	10, 50, 75, 100	Girdled, Dead
	Glischrochilus siepmanni W.J.Brown	Fungivore	10, 20, 50	Girdled, Dead
	Glischrochilus vittatus (Say)	Predator	10, 50	Dead
Ptiliidae	*Acrotrichis castanea* (Matthews)	Fungivore	10, 20, 50, 75, 100	Girdled, Dead
	Ptinus fur (Linné)	Fungivore	50	Dead
Pyrochroidae	*Dendroides ephemeroides* (Mannerheim)	Fungivore	20, 75	Girdled
Rhizophagidae	*Rhizophagus brunneus* Horn	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Rhizophagus dimidiatus Mannerheim	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Rhizophagus remotus LeConte	Predator	10, 20, 50, 75	Girdled, Dead
Scolytidae	*Carphoborus andersoni* Swaine	Wood- and bark- borer	10	Dead
	Cryphalus ruficollis Hopkins	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Crypturgus borealis Swaine	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Dendroctonus rufipennis (Kirby)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Dryocoetes affaber (Mannerheim)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Dryocoetes autographus (Ratzeburg)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Ips borealis Swaine	Wood- and bark- borer	20	Girdled
	Ips mexicanus (Hopkins)	Wood- and bark- borer	75	Girdled
	Ips pini (Say)	Wood- and bark- borer	10, 20, 50, 75	Girdled, Dead
	Phloeotribus lecontei Schedl	Wood- and bark- borer	10, 100	Dead
	Pityogenes plagiatus plagiatus (LeConte)	Wood- and bark- borer	10, 20	Dead
	Pityokteines ornatus (Swaine)	Wood- and bark- borer	10, 20, 50	Girdled, Dead
	Pityophthorus spp.	Wood- and bark- borer	10, 20, 50, 75	Girdled, Dead
	Polygraphus rufipennis (Kirby)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Scierus annectans LeConte	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Scierus pubescens Swaine	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Scolytus piceae (Swaine)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Trypodendron lineatum (Olivier)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead

Family	Species	Feeding group	Harvesting treatment	Trap treatment
	Trypodendron retusum (LeConte)	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
	Trypodendron rufitarsis (Kirby)	Wood- and bark- borer	50, 75	Girdled, Dead
	Xylechinus montanus Blackman	Wood- and bark- borer	10, 20, 50, 75, 100	Girdled, Dead
Scydmaenidae	*Euconnus* pb.*semiruber* Casey	Predator	20	Dead
Staphylinidae	*Acidota crenata* (Fabricius)	Predator	10, 50, 75, 100	Girdled, Dead
	Anotylus sobrinus (LeConte)	Scavenger	10, 20	Girdled, Dead
	Bisnius tereus Smetana	Predator	20, 50, 75, 100	Girdled, Dead
	Deinopteroloma subcostatum (Maklin)	Predator	100	Girdled
	Gabrius brevipennis (Horn)	Predator	10, 20, 75, 100	Girdled, Dead
	Heterothops fusculus LeConte	Predator	20, 50, 75	Girdled, Dead
	Ischnosoma splendidum (Gravenhorst)	Predator	10	Dead
	Lathrobium washingtoni Casey	Predator	75	Girdled
	Lordithon bimaculatus (Couper)	Predator	100	Dead
	Lordithon fungicola Campbell	Predator	10, 20, 50, 75	Girdled, Dead
	Lordithon longiceps (LeConte)	Predator	100	Dead
	Megarthrus sinuaticollis Boisduval & Lacordaire	Fungivore	10, 20, 50, 75	Girdled, Dead
	Micropeplus laticollis Maklin	Fungivore	75, 100	Girdled
	Mycetoporus americanus Erichson	Predator	10, 50	Girdled, Dead
	Nudobius cephalus (Say)	Predator	10, 20, 50, 75	Girdled, Dead
	Olisthaerus sp	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Omalium foraminosum Maklin	Predator	0, 50, 75, 100	Girdled, Dead
	Phloeostiba lapponicus (Zetterstedt)	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Pseudopsis sagitta Herman	Predator	10, 20, 50, 75	Girdled, Dead
	Pseudopsis sp.	Predator	10, 50	Girdled, Dead
	Quedius criddlei (Casey)	Predator	75	Girdled
	Quedius frigidus Smetana	Predator	50	Dead
	Quedius plagiatus Mannerheim	Predator	10, 50, 75, 100	Girdled, Dead
	Quedius rusticus Smetana	Predator	10, 20, 50, 75, 100	Girdled, Dead

Family	Species	Feeding group	Harvesting treatment	Trap treatment
	Quedius simulator Smetana	Predator	10, 50, 75, 100	Girdled, Dead
	Quedius velox Smetana	Predator	10, 20, 50, 75, 100	Girdled, Dead
	Siagonium punctatum LeConte	Scavenger	10, 20, 75	Girdled, Dead
	Staphylinus pleuralis LeConte	Predator	20, 50	Girdled, Dead
	Stenus reconditus reconditus (Casey)	Predator	75	Girdled
	Tachinus frigidus Erichson	Fungivore	20, 50, 100	Dead
	Tachyporus borealis Campbell	Predator	10	Dead
	Tachyporus canadensis Campbell	Predator	10	Dead
Trogositidae	*Ostoma ferruginea* (Linné)	Fungivore	10, 20, 75, 100	Girdled, Dead
	Thymalus marginicollis Chevrolat	Predator	75	Dead

Chapter 5 General Discussion

In this thesis I underscore that course woody debris (CWD) is an important factor influencing saproxylic beetle assemblages. Two major themes regarding CWD flow from my analyses: 1) girdling trees to create snags very early in decay appears to support assemblages of beetles quite different from those in any of the natural snags sampled, and 2) amount of CWD in surrounding habitats influences the colonization of anthropogenic CWD by beetles. Furthermore, like researchers elsewhere, I show that a unique assemblage of beetles is attracted to fire-killed trees and suggest that this fauna could be threatened by effective fire suppression to maintain harvestable timber. Forest harvesting has a large effect on these variables by reducing the total amount of CWD in the forest and changing the age and size distribution of CWD. Therefore, in principle, it is indeed possible to optimize forest management in relation to the conservation of saproxylic assemblages and the maintenance of other desired forest values once there is agreement about tolerable changes to the assemblages.

5.1 Main Findings of the Thesis

The first chapter of this thesis highlighted the need for study of saproxylic organisms. Studies from Europe have demonstrated the adverse effects on saproxylic beetles caused by centuries of forest harvest. These studies suggest that the loss of CWD in managed forests, due to forest harvest, is the main threat to maintaining healthy saproxylic beetle communities.

My second chapter examined a representative saproxylic beetle assemblage across a forest cover type gradient and recognized numerous structural features of natural forests that likely effect saproxylic beetle assemblages. These features are summarized in the multivariate regression tree (Fig. 2-12). This analysis indicated that the most important factor affecting saproxylic beetle assemblages in natural forests is the stand-level volume of white spruce downed wood debris (DWD). Stands with less than $0.25m^3$/ha of white spruce DWD, which were mostly deciduous dominated stands, had dramatically different saproxylic beetle assemblages than those stands with at least the threshold amount of white spruce DWD. Other factors affecting saproxylic beetle assemblages, in order of importance are: 1) how and when the tree died; 2) stand level volumes of balsam poplar; 3) tree species, and 4) number of snags within a 5m radius of the trap.

My work suggests that these five factors are crucial to establishing the natural variability of saproxylic beetle communities in the Canadian boreal mixedwood forest. Further understanding the factors that determine saproxylic beetle communities will enhance our ability to predict the impacts of disturbances on these communities.

My third chapter identified a unique group of pyrophilous species from both saproxylic and epigaeic beetle communities of the boreal mixedwood in western North America. Furthermore, the chapter identified numerous other disturbance-adapted beetles that are attracted to fires and other disturbances. Several distinct assemblages of beetles were noted within the burn, depending on the severity of the burn. Although only 2 species of beetles (*Sericoda quadripunctata* and *Sericoda bembidioides*) were considered to be truly pyrophilous, 13 epigaeic and 12 saproxylic species were statistically significant indicators of severely burned forests.

Habitat features that make recently burned stands attractive to certain species have not been clearly defined. Wikars (1992) stated that wildfire alters beetle assemblages by increasing the amount of CWD, changing the decay rate of CWD and by creating a temporarily-competition-free environment. For some species, congregating in burned areas may increase the probability that they will find mates and reproduce successfully (Evans 1971). Although the pyrophilous nature of *Sericoda* spp. has been known for decades, it is unknown how these beetles detect recently burned stands, or which characteristics of burned habitats are Esseential for their success. Wikars (1995) reported that clear-cutting before a site is burned prevents the establishment of *S. quadripunctata*, suggesting that this species needs the large amount of burned CWD created after a wildfire. Furthermore, it is known that burned habitats are suitable for *Sericoda* spp for only 1-2 years. *Sericoda* spp were collected in greatest numbers in the first year following the burn and declined in abundance by the second year, a pattern also observed by Holliday (1984, 1991, 1992). Therefore, CWD qualities are important in determining beetle assemblages following wildfire, but faunal succession occurs very rapidly.

My fourth chapter focuses on the short term impacts of variable retention (VR) harvesting on saproxylic beetle assemblages. VR harvesting is a relatively new technique of leaving more residual structure on harvested landscapes in order to add structural complexity to the landscapes (Franklin et al. 1997). My study revealed little immediate effect of VR harvesting on saproxylic beetle assemblages. VR treatments employed at EMEND had minor short-term impacts on the CWD available at the harvested sites, and therefore, may have been relatively unimportant to saproxylic beetle assemblages given the existence of a large species pool in the surrounding forest. As the EMEND stands age, however, input of CWD will differ depending on the volume of residual trees left in particular stands, and the long term benefits of VR harvesting may become more evident.

Although the effects of differences in residual structure under VR harvesting were minimal for saproxylic beetle communities as a whole, some groups appeared to show effects of the treatment. Structure of the fungivore community, for example, appeared to be slightly affected 1.5 years following harvest and more profoundly affected 2.5 years after harvest. These beetles are generally small in size, feed on molds and their composition could easily reflect changes in the fungal communities at these sites. In addition, other small-bodied, tree-feeding beetles (*Xylechinus montanus* and *Pityophthorus* spp.) also appeared to be negatively affected as harvesting intensity increased. VR harvesting did influence the saproxylic beetle assemblage, but until the changes in stand level volumes of CWD become more evident the actual benefits for saproxylic beetles will not be realized.

5.2 Importance of Coarse Woody Debris (CWD)

It is clear that modern industrialized forest harvest greatly reduces the total volume of CWD and that the greatest reductions are in large diameter CWD (Siitonen et al. 2000). This reduction of CWD is probably the most significant difference between forest harvest and any kind of natural disturbance. Historically, natural disturbances (*e.g.*, wildfire, wind and insects) created large pulse inputs of CWD in forested stands, but these tended to be eliminated as landscapes were brought under harvest rotation. Studies from Fennoscandia, for example, have found that managed forests had 90-98% less CWD than unmanaged forests (Siitonen et al. 2000).

Studies from Fennoscandia have shown a dramatic drop in saproxylic beetle diversity between managed and old growth forests (Økland and Haagvar 1994, Siitonen and Martikainen 1994, Martikainen et al. 2000). Furthermore, Martikainen et al. (2000) found a simple regression model where the logarithmic volume of CWD explained most of the species richness of saproxylic beetles.

Forestry companies are just now starting to realize the importance of CWD for protecting biological diversity on forested landscapes and have begun taking measures to increase the retention of live trees after harvesting. In European countries, foresters are even creating CWD immediately after harvest by topping trees to create standing snags (Schroeder et al. 1999).

5.3 Saproxylic beetle definition and sampling methods.

As "saproxylic" species have been subject to increasing attention from conservationists in recent years, there is a growing need to clearly define what sorts of species should be included. Speight (1989) stated that saproxylic species are those that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylic organisms. The term "depend" in the strictest sense means that these insects would not survive without the presence of CWD, and is easily interpreted for species that colonize, occupy and reproduce in dead wood. Many of these species (e.g., *Trypodendron lineatum*), however, are also known to colonize and reproduce in living trees, some killing the tree in the process. The definition becomes even harder to interpret when considering predators. Some predators specialize on wood boring insects (*e.g.*, Cleridae) but many others are generalist predators that will eat whatever is available, including saproxylic insects, and it is largely unknown how the responder populations would fare if truly saproxylic species disappeared.

Because large scale experiments that remove CWD from forested stands have not been undertaken and are unlikely in the near future, researchers rely on detailed information about substrate requirements published in hundreds of journal articles to designate species as saproxylic. Many of these articles are based on behaviour of a few individuals and the range of suitable substrates and feeding characteristics that broadly characterize a species are not known. Therefore, it is difficult to determine if species are truly dependant on dead wood and would not survive without it.

In the fourth chapter of this thesis I have grouped putative saproxylic species based on feeding behavior or substrate requirements. It is much easier to identify whether an insect feeds on fungus or reproduces in wood, than to determine if that insect would not survive in the presence of CWD. This approach allows better resolution as to which group(s) is/are being affected by harvest and may allow us to better adjust forest management to minimize negative impacts on these groups. If the term 'saproxylic' is to remain valuable, its definition should come to include the degree of dependency an organism has on CWD. Furthermore, use of more specific functional groups (*e.g.*, fungivore, predator) of saproxylic species may allow us to reach more ecological sensitive interpretations of results from these types of studies.

5.4 Management recommendations and future research

Deciduous dominated boreal stands are generally poorly studied in other parts of the world because few stands remain after long periods of intensive management and stand conversion. Recent studies emerging from North America (Hammond 1997, Hammond et al. 2001, Hammond et al. 2004) show that deciduous stands have a unique and diverse saproxylic community and complement extrapolations from some European work (Ahnlund 1996). The lack of extensive deciduous stands in the boreal forests of other parts of the world should increase the importance conservation efforts in these stands in North America. The importance of deciduous trees in conservation of saproxylic organisms has been recognized in northern Europe (Martikainen 2001).

It is clear from this thesis and studies from Fennoscandia (Siitonen 2001) that both CWD quality and quantity, and the relative abundance of canopy trees have strong effects on saproxylic beetle assemblages. Conservation of saproxylic faunal elements will require retention of the full range of cover types on the forest landscape. There is therefore a need to identify the specific qualities and quantities of CWD Esseential to maintaining diverse saproxylic beetle communities. Present understanding suggests that this will not be a short list. Our present data suggest that all distinct boreal stand types within the mixedwood successional sequence will be associated with somewhat distinct saproxylic communities. These likely originate in the subtleties of CWD succession in different mixes of tree species. In order to conserve this ecologically important group of insects and retain its functions in nutrient cycling, we must aim to retain appropriately scaled mixes of all natural cover types on forested landscapes.

This study and others (Hammond et al. 2001, Siitonen 2001, Hammond et al. 2004) demonstrate that there is an initial wave of beetles that colonize burned areas. This community is made up of species that are either fire-adapted or more generally disturbance-adapted. It is largely unclear in current literature exactly what role fire-adapted species may play in forest processes such as decomposition and nutrient cycling. In a strict conservation sense, existing data suggest that fires have to be maintained at natural intervals on the landscape in order to conserve these fire-adapted species. In a management sense these insects may play important roles in the recovery of these disturbed areas to return them to pre-disturbance conditions. We seek to meet this objective by attempting to emulate critical aspects of natural disturbance through forest management practices. In the case of fire-adapted species, large-scale fires, which seem to be inevitable in western Canada, may cushion these species against extinction. However, if we wish to build their functions into most successional sequences, there may be no alternative but to introduce some burning into stand regeneration activities.

The benefits of VR harvesting on saproxylic beetles cannot be fully evaluated at this time. Considering only short term impacts apparent from the EMEND experiment, partially cutting the forest reveals no benefits for the conservation of saproxylic beetles. Ultimately, benefits of VR will depend on cutting a smaller portion of many stands having advantages over cutting a large proportion of fewer stands. Benefits of VR for saproxylic beetles are anticipated to become more evident at EMEND as these stands age and the impact of local legacy elements is felt. At this point the amount (and possibly quality) of CWD will begin to diverge more significantly and faunal effects are predicted. Although we have clear evidence that there are lower limits to volume of CWD required to support a rich saproxylic fauna (Siitonen & Martikainen 1994), the implications of variation in CWD produced across landscapes by forestry activities remain to be thoroughly studied.

Literature Cited

Ahnlund, H. 1996. Saproxylic insects on a Swedish dead aspen. Entomologisk Tidskrift **117**:137-144.

Evans, W. G. 1971. The attraction of insects to forest fires. *in* Proceedings of the Tall Timbers Research Station, Tallahasse, Fl.

Franklin, J. F., D. A. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Island Press, Washington, D.C.

Hammond, H. E., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research **31**:1175-1183.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. Canadian Entomologist **129**:1009-1033.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research **34**:1-19.

Holliday, N. J. 1984. Carabid beetles (Coleoptera, Carabidae) from a burned spruce forest (*Picea* Spp). Canadian Entomologist **116**:919-922.

Holliday, N. J. 1991. Species responses of carabid beetles (Coleoptera, Carabidae) during postfire regeneration of boreal forest. Canadian Entomologist **123**:1369-1389.

Holliday, N. J. 1992. The carabid fauna (Coleoptera, Carabidae) during postfire regeneration of boreal forest - properties and dynamics of species assemblages. Canadian Journal of Zoology **70**:440-452.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletin **49**:205-218.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation **94**:199-209.

Økland, B., and S. Haagvar. 1994. The insect fauna associated with carpophores of the fungus Fomitopsis pinicola (Fr.) Karst. in a southern Norwegian spruce forest. Fauna Norvegica, Series B **41**:29-42.

Schroeder, L. M., J. Weslienb, Å. Lindelöwa, and A. Lindhe. 1999. Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting. Forest Ecology and Management **123**:21-30.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins **49**:11-41.

Siitonen, J., and P. Martikainen. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russion Karelia. Scandinavian Journal of Forest Research **9**:185-191.

Siitonen, J., P. Martikainen, P. Punttila, and J. Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management **128**:211-225.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe Publications, Strasbourg.

Wikars, L. O. 1992. Forest fires and insects. Entomologisk Tidskrift **113**:1-11.

Wikars, L. O. 1995. Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera:Carabidae). Annales Zoologici Fennici **32**:375-384.